The effect of climatic variables on the demography and behaviours of banded mongooses (*Mungos mungo*)

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Swansea University 2023

Submitted to Swansea University in fulfilment of the requirements for the Degree of Doctor of Philosophy

Abstract

Human-induced climate change negatively affects animal reproduction and survival. Understanding vulnerability to climate change requires knowledge on how animals respond to changes in environmental conditions. Here, I used a long-term (>20 years) dataset of climatic, life-history and behavioural data on a wild population of banded mongooses to investigate how environmental change will affect this cooperatively breeding equatorial mammal. Using time series decomposition, I show how reproduction and early-life survival is affected by rainfall and temperature at varying timescales (seasonal, long-term trends, and short-term variation). Births occur year-round, but reproduction is usually timed so that females either conceive or give birth during the wet seasons where food is most plentiful (Chapter 2). Next, I used structural equation modelling to investigate both direct effects of environmental conditions on early-life survival and indirect impacts via changes to cooperative behaviour (Chapter 3). High levels of rainfall boosted helping effort, which in turn increased pup survival, but high temperatures had both direct and indirect negative effects on survival. I found no evidence for a buffering effect of cooperative social groups on harsh environmental conditions, which has been previously suggested for other species. Chapter 4 presents support for high temperatures limiting offspring growth via the heat dissipation limit hypothesis, which predicts that high temperatures limit metabolic expensive processes such as lactation, due to inability to disseminate the additional heat produced. Finally, banded mongooses behaviourally thermoregulate by resting more and foraging less under high temperatures (Chapter 5). However, this is insufficient to mitigate increases in body surface temperatures. Overall, my results suggest that banded mongooses should suffer from rising temperatures with limited or no relief via behavioural adjustments or social buffering. However, predicted increases in rainfall may partially mitigate these impacts, highlighting the challenging complexity in predicting overall effects of climate change on wild animal populations.

Declarations and Statements

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed ....[redacted]...................................... (candidate)

Date ....30/10/2023...

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

Signed ......[redacted]... (candidate)

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I hereby give consent for my thesis, if accepted, to be available for electronic sharing.

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The University's ethical procedures have been followed and, where appropriate, that ethical approval has been granted.

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Acknowledgments

First and foremost, I would like to thank my Lord and Saviour Jesus Christ for His unfailing love.

I would also like to thank my supervisors Hazel Nichols and Kevin Arbuckle for their continuous support throughout my PhD. They have truly gone above and beyond what is required of them, and I not only appreciate their guidance and advice but also their friendship over the last three years. I have enjoyed our countless random conversations (which I will refrain from mentioning here) and whilst unsuccessful, I do appreciate Hazel's many attempts at trying to get me to eat healthier. I would also say that nothing cements a friendship quite like being stuck outside at night in the middle of a national park with various predators lurking nearby. I'm sure Hazel appreciated my attempt to make light of the situation by casually mentioning that I just needed to outrun her should any predator appear (not that I ever would of course!). I'm super grateful to Kevin who's knowledge of R far exceeds my own, for not only helping me trouble shoot coding errors but also for sharing my sense of humour which usually causes people to roll their eyes.

Many thanks go to the people responsible for the banded mongoose project over the years including Mike Cant and Francis Mwanguhya. I am grateful to all of the field staff that have been/ are responsible for the ongoing data collection for over 20 years now, without them there would be no life history or behavioural data for me to work with. Also, a huge thanks to Onismus Bwamale for helping to identify the mongooses during my field trip to Uganda, I would not have been able to collect half as much data without him.

I want to thank my Lifepoint church family for being my home away from home. They have shown me so much love and have helped me in more ways than I could say, and I will always be grateful to them for this. Thanks to my close friends Jordan Sydenham, Justin Biddle, Man Yin Leung, Daniel Whitesman and Samuel Prosser. They have been there for me through my highs and lows and helped me to grow as a person. They have also listened to me when I go on mini rants about random things (which is a testament to their patience). Thanks also to my office mates over the years, Nathan Thomas, Jack Cooper, Kasper Bandit, Jordi Solà, Megan Nicholl and many others. I have really appreciated being able to share ideas, trouble shoot R together and vent about the stresses that come with doing a PhD. Apologies for anyone that feels left out but if you are close enough to me to be mentioned you should also know just how forgetful I am.

There have also been two important comforts that have been crucial in helping me to get through my PhD; the first of which is Friends, the greatest and funniest TV show to ever air. The second is

Yorkshire tea and I am looking forward to the near future where I will hopefully be able to afford Yorkshire gold. I would also like to give a special shoutout to my supervisors' dog Eevee for providing me with a much needed distraction from both my worries and my work. I hope I will continue to be her favourite human for a very long time.

Finally, I would like to thank my family, particularly my mum for being there for me throughout my studies. I hope one day to give back to her everything that she has given to me. I also want to take this moment to put her mind at ease and assure her that I will stop pursuing any more degrees and put all of my efforts into getting myself a job.

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Paper 1 (Small increases in ambient temperature reduce offspring body mass in an equatorial mammal)

Located in Chapter 4

Candidate primarily developed the initial concept, conducted the analysis, and wrote the initial manuscript. Author 1 and 2 helped to design the study, discussed ideas about conducting the analysis and provided revisions to the manuscript. Authors 3, 4, 5, 6 and 8 run the banded mongoose project and oversaw the collection of the field data used in the study. Authors 7 and 8 gained funding for the long-term study and provided comments, helping to improve the manuscript.

1 Introduction

1.1 The impacts of anthropogenic climate change on animal populations

Human-induced global climate change has caused temperatures to rise by 0.89°C between 1901-2013, and under most climate change scenarios, temperatures are expected to continue rising by 1.5-2°C (relative to the 1850-1900 period) before the end of 2040 and by 1.5-4.8°C by 2100 (IPCC 2022; IPCC 2013). In addition to long-term changes in temperature, climate change has also increased the frequency of extreme weather events such as storms, cyclones, and wildfires (IPCC 2022). Heatwaves are also predicted to not only increase in frequency, but also get longer and become more severe over time (Meehl & Tebaldi 2004). Furthermore, whilst rainfall is increasing in some areas, increasing the risk of floods, other areas are experiencing less rainfall over time leading to more droughts (IPCC 2022). Aside from long-term and short-term impacts of climate change, regular seasonal patterns have also been disturbed. For example, in the northern hemisphere the timing of spring has shifted earlier by approximately 2.8 days per decade (Parmesan 2007).

These changes in environmental conditions have been shown to cause animal population declines, reduce survival and fecundity, increase the spread of invasive species, cause shifts in the distribution of species (Mawdsley *et al.* 2009) and alter morphology and growth (Ozgul *et al.* 2009; Lackey & Whiteman 2022). Given our rapidly changing climate, assessing the impact of environmental conditions on animal populations is crucial for predicting future responses, as well as planning conservation and management strategies (McCarty 2001; Laws & Belovsky 2010).

Reproduction and early life survival are crucial life history stages shown to be susceptible to changes in short-term (Boersma & Rebstock 2014), seasonal (Parmesan 2007; Bronson 2009), and long-term changes in environmental conditions (Abrahms *et al.* 2022). For example, during short-term droughts, female baboons (*Papio cynocephalus*) are found to be less likely to conceive and carry pregnancies to term (Beehner *et al.* 2006). Climate change can also affect the seasonal reproduction of multiple species by causing a mismatch between the timing of births and optimum foraging conditions due to the earlier onset of spring (Bronson 2009). Though some species such as tree swallows (*Tachycineta bicolor*) (Dunn & Winkler 1999) and red deer (*Cervus elaphus*) (Moyes *et al.* 2011) have managed to adapt their reproductive timing, other species including roe deer (*capreolus capreolus*) have continued to give birth at the same time, with negative consequences for survival (Plard *et al.* 2014). Long-term increases in temperature have also resulted in parturition being delayed and reduced litter sizes in wild dogs (*Lycaon pictus*) (Abrahms *et al.* 2022). In order to accurately determine the effect of climate change on reproduction in animal populations, we need to both disentangle and investigate the impact of climate change at all three time-scales; seasonal, short-term and long-term.

Most endotherms use physiological and/or behavioural mechanisms in order to thermoregulate, controlling heat gain and heat loss (Boyles *et al.* 2011; Terrien *et al.* 2011). The four principle methods of heat loss are radiation, convection, conduction and evaporation, and as metabolic heat reaches the surface of the skin, it must leave through one of these mechanisms to avoid dangerous hyperthermia (Gagge & Gonzalez 2010; Tansey & Johnson 2015). Heat transfer is affected by various environmental conditions including ambient temperatures, humidity, wind speed and solar radiation (Mitchell *et al.* 2018). Anthropogenic-induced increases in temperature are therefore likely to influence thermoregulation in natural animal populations. As ambient temperatures get closer to body surface temperatures, it becomes harder for metabolic heat to be dissipated, and animals may be forced to change their exothermic physiological processes accordingly; this is known as the heat dissipation limit theory (Speakman & Król 2010). In support of this theory, milk production, which is an extremely exothermic process (Król & Speakman 2003b, a) declines in multiple species under hot condition, with negative consequences for offspring mass (Johnson & Speakman 2001; Renaudeau & Noblet 2001; Król & Speakman 2003b; Zhao *et al.* 2020). Animals can however adapt their behaviours in order to thermoregulate, for example by reducing the ambient temperatures they are exposed to by choosing cooler microsites (Wolf & Walsberg 1996; Giotto *et al.* 2013; Lopes & Bicca-Marques 2017) or increasing the rate of conductive and evaporative heat loss by wallowing or covering their body in mud or water (McKay 1973; Mota-Rojas *et al.* 2021). Animals can also reduce their own metabolic heat production by reducing activity levels (Cain III *et al.* 2006). It is important to identify whether and/or how animals thermoregulate in order to predict responses to future increases in temperature.

Whilst there have been numerous studies investigating the effect of climate change on animals in mid-high latitudes, relatively little attention has been given to equatorial regions (Feeley & Silman 2011). Indeed, species living at higher latitudes have generally thought to be the ones most affected by climate change (Post *et al.* 2009; Plard *et al.* 2014). This may in part be due to the fact that global warming is most evident at higher latitudes with relatively small increases in temperatures seen in tropical/equatorial regions (IPCC 2007). Taken together with the fact that there is very little seasonality (variation in temperature) with regards to temperature in equatorial regions (Carroll *et al.* 2015a), on face value the impact of temperature change in equatorial regions seems insignificant. This line of thinking however dismisses the fact that equatorial animal populations at low altitudes are adapted to living under relatively constant temperatures and so may have a narrow range of thermal temperature under which they can thrive (Tewksbury *et al.* 2008; Bozinovic 2011). Because of this, even small changes in temperature could have strong adverse effects on their populations (Janzen 1967; Wright *et al.* 2009). Furthermore, whilst at mid-high latitudes overall yearly rainfall has increased over time since 1900, in tropical and subtropical regions, rainfall has gradually declined (Houghton 1996). This is worrying for many tropical species where rainfall is highly associated with food availability (Bronson 2009), and therefore may have strong impacts on reproduction and survival. More studies investigating the effect of current changes in rainfall and temperature on tropical species are then needed in order for us to better understand how they will react to future long-term changes in climate.

1.2 Potential buffering of climate-related impacts through cooperation

The way in which animals behave in response to climate change is likely to play a large role in determining how vulnerable they are to current and future changes (Huey *et al.* 2012; Mason *et al.* 2014; Sunday *et al.* 2014). One behavioural trait typically associated with harsh, unpredictable environmental conditions, particularly where rainfall fluctuates strongly over time, is cooperative breeding (Cockburn & Russell 2011; Jetz & Rubenstein 2011). This occurs in social groups where subordinate ‘helpers’ aid the dominant breeders in raising their offspring (Solomon & French 1997; Koenig & Dickinson 2016). This allows groups to mitigate against the adverse effects of changing environmental conditions (Rubenstein & Lovette 2007; Jetz & Rubenstein 2011) and reduce the cost breeders face whilst reproducing (Solomon & French 1997; Koenig & Dickinson 2016). For example, in tropical regions where rainfall is usually a proxy for food availability, during periods of low rainfall helpers can reduce parental workload by providing food for the offspring (Covas *et al.* 2008). This is shown to occur in the sociable weaver (*Philetairus socius*) and not only do helpers improve offspring body condition, but they also allow parents to produce more offspring under harsh conditions (Covas *et al.* 2008).

Some evidence for buffering against harsh conditions comes from evolutionary studies of cooperative breeding (Shen & Rubenstein 2019). For example, the ‘load-lightening’ hypothesis suggests that by spreading the cost of raising offspring over multiple individuals, breeders are able to successfully reproduce even when conditions are suboptimal (Sarhan & Kokko 2007). This leads to the prediction that larger groups with more helpers will do better than smaller groups under harsh environmental conditions. Indeed, large groups are found to buffer against the negative effects of low rainfall on fecundity, pup growth and pup survival in meerkats (*Suricata suricatta*) (Groenewoud & Clutton-Brock 2021) and it is suggested that this may be because they can defend larger, higher quality territories as well as provide better care to pups (Krause *et al.* 2002; Dyble *et al.* 2019). Another hypothesis based on load-lightening is called the ‘bet-hedging’ strategy which suggests that under unpredictable conditions, cooperative breeding can improve the reproductive success of groups by allowing some individuals to successfully reproduce even when conditions are harsh by spreading the cost over multiple helpers (Rubenstein 2011). As a result, interannual variation in reproductive success is reduced despite high environmental variability. Supporting this, cooperatively breeding birds (Cornwallis *et al.* 2017) and mammals (Lukas & Clutton-Brock 2017) are found to be strongly associated with harsh, unpredictable environments on a global scale.

While the evolution of cooperative breeding may be associated with harsh environments, other factors may contribute to its evolution. For example, it has been proposed that the evolution of cooperative breeding could be associated with factors that link to the benefits or costs of delayed reproduction and allomaternal care (Lukas & Clutton-Brock 2012). In line with this, the 'benefits-of-philopatry' hypothesis suggests that in some cases, non-breeding helpers are better off staying in their natal group, potentially because it allows them to inherit a higher-quality territory, reduces the risk of predation during dispersal, and they may benefit from being more familiar with their natal territory allowing for greater feeding efficiency (Ekman *et al.* 2001; Clutton-Brock & Lukas 2012). This hypothesis can also be linked to the 'ecological constraints' hypothesis which suggests that ecological constraints can reduce the likelihood of individuals that disperse from their natal group being able to successfully reproduce (Stacey & Ligon 1991). These constraints could include a lack of potential mates, the inherent risks of living alone, a low probability of independent breeding and a lack of unoccupied breeding territories, also known as 'habitat saturation' (Nelson-Flower *et al.* 2018). Finally, cooperative breeding may be the 'best-of-a-bad-job', defined by situations where individuals (usually males) that are at a competitive disadvantage compared to dominant individuals, use unconventional reproductive tactics to gain some reproductive fitness (Shuster 2010). In the case of cooperative breeding, individuals may choose to help others because they are constrained from reproducing on their own (Dickinson & Hatchwell 2004; Jetz & Rubenstein 2011); in this way this strategy is similar to the 'ecological constraints' hypothesis.

1.3 Banded mongooses as a study system for understanding climate impacts

In this thesis, I investigate the impacts of short-term, long-term and seasonal changes in temperatures and rainfall on an equatorial species; the banded mongoose (*Mungos mungo*). This species is a cooperative breeder, allowing me to investigate the extent to which buffering through offspring care can reduce the negative impact of harsh conditions.

1.3.1 Study population

Banded mongooses are small (~1.5kg) diurnal cooperative mammals belonging to the family Viverridae (Cant *et al.* 2016). Banded mongooses can be found across sub-Saharan Africa (Cant & Gilchrist 2013), however our study population resides in and around Mweya peninsula, Queen Elizabeth National Park, Uganda (0°12′S, 27°54′E) (Fig 1).

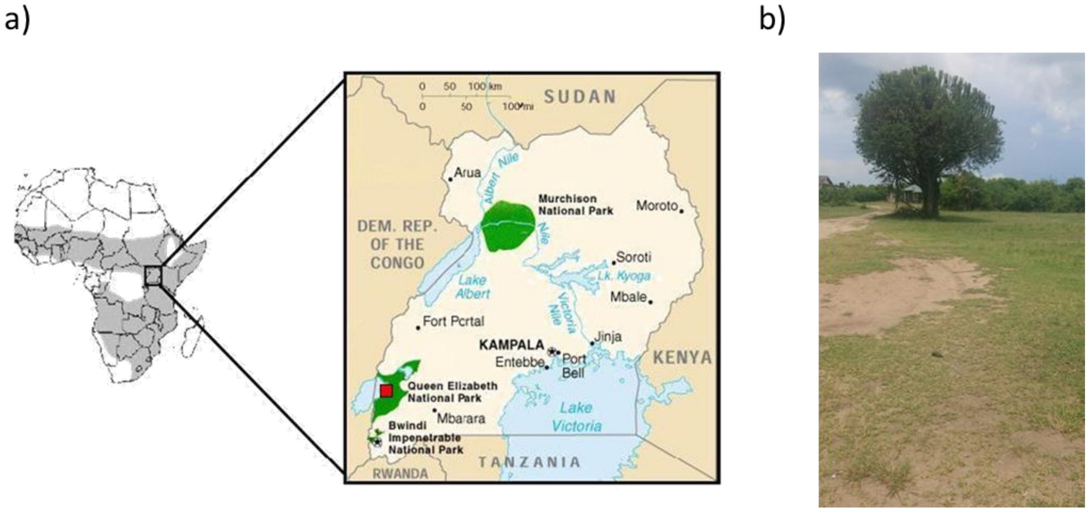


Figure 1. a) An image illustrating the location of Mweya peninsula, Queen Elizabeth National Park, Uganda (0°12′S, 27°54′E) where the banded mongoose population is located and b) an image showing the habitat they frequent.

This study site can be characterised as a scrub-savannah habitat. At any one time the population usually consists of ~250 individuals split into 10-12 mixed family groups (Cant *et al.* 2013, 2016). The banded mongooses within our study population are habituated to observers at <10 m (usually <5 m) though some groups are habituated to closer observation (Jordan *et al.* 2010). Social groups are generally stable and have a male-biased sex ratio at all age classes (Rood 1975; Cant *et al.* 2016). They also have some of the largest group ranges of any social mammal, from 5 to 75 individuals, though most social groups consist of 10-30 adults (Cant 2000; Cant *et al.* 2016). Social groups within the population are visited every 1-3 days in order to collect data on life history and group composition (Thompson *et al.* 2017).

This study system presents a rare opportunity to study the effects of changing climatic conditions on equatorial cooperative breeders due to the long-term data available. Life history data has been collected since November 1991 and we have a total of 20,714 life history events recorded across 4731 individuals. These life history events include when each individual is born (or first seen if they immigrated into the population an adult), if and when they immigrate to a new group, when females go into oestrus and subsequently give birth or abort their litters. It also includes information about when and how each individual dies or is last seen. This dataframe also contains group-level information such as when groups interact with other groups, when groups form and when groups split via the eviction of a subset of subordinate individuals. We also had access to daily rainfall (mm) and maximum temperature (°C) data from the Mweya meteorological station located in the middle of our study site since April 1999.

1.3.2 Foraging behaviour

Banded mongooses are generally insectivorous with their main prey being millipedes and beetles, though ants, termites, crickets and earwigs are also consumed. They have also been known to feed on small invertebrate prey, fruit, eggs and even human refuse when given the chance (Rood 1975; Gilchrist *et al.* 2004). Groups normally forage together twice a day, and although they undertake these trips together, they forage individually and defend their catch from other individuals (De Luca & Ginsberg 2001). Groups have multiple dens within their territory and switch dens every few days (Cant *et al.* 2013). All of the members of a group sleep in the same den and begin their first foraging trip just after the break of dawn which lasts between three to four hours (Cant *et al.* 2013). Whilst foraging they use their sense of smell to find prey which are normally hidden in dung, leaf litter or within a few inches of soil, in which case banded mongooses use their forepaws to dig (Cant *et al.* 2013). After the first foraging trip, the group finds a shaded area to rest and then resumes foraging in the late afternoon for two to three hours until sunset (Cant *et al.* 2013).

1.3.3 Reproduction

Each social group contains a core of dominant breeders (usually between 1-5 males and 3-7 females) which reproduce 3-4 times a year, although subordinates breed alongside them when conditions allow for it (Cant 2000; Bell 2010; Nichols *et al.* 2012b). Banded mongooses have a gestation period of ~3 months and births have been found to occur year-round, though they are not evenly distributed throughout the year. Within groups, females reproduce synchronously, giving birth together (usually on the same day) and the individual litters are raised as one large communal litter in an underground den (Gilchrist 2006b). The evolution of this extreme birth synchrony is thought to be the result of the cost of giving birth earlier or later than the other birthing females (Hodge *et al.*

2011). Pups that are born too early are at higher risk of infanticide by pregnant females as in these cases maternity is clear, whilst those that are born too late risk being outcompeted by older, bigger littermates (Cant *et al.* 2013). As a result, females within a group give birth at the same time, "scrambling" cues to parentage (Hodge *et al.* 2011), and prior to emergence the pups feed indiscriminately from all lactating females (those that gave birth into the communal litter). Pups remain in the den for their first ~30 days, after which they start going on foraging trips with the rest of their groups and begin transitioning from milk to solid food (Cant *et al.* 2016).

Pregnancies can normally be identified at around 40 days after conception due to the visible swelling of the abdomen and weight gain, and these observations are sometimes confirmed through ultrasound scans and/or palpitations of the abdomen (Cant 2000; Gilchrist 2006a; Inzani *et al.* 2019). Birth dates are identified when pregnant females are missing from morning foraging trips, when the size of their abdomen returns to normal and when babysitting is first observed (Gilchrist 2006a; Hodge *et al.* 2011).

1.3.4 Eviction and dispersal

Individuals of both sexes typically show a high level of natal philopatry, remaining in their natal group even after becoming sexually mature at around 1 year old (Cant *et al.* 2013, 2016). Indeed, 85% of individuals never disperse from their natal group (Cant *et al.* 2016), and even those that do disperse normally breed within their natal group beforehand (Nichols *et al.* 2010; Cant *et al.* 2013). As a result, there is a high degree of inbreeding within groups with 66.4% of individuals having a non-zero breeding coefficient and 7.1% of individuals being the result of first-order inbreeding (Wells *et al.* 2018). The level of inbreeding within groups however is still lower than would be expected if they mated randomly, suggesting some kind of inbreeding avoidance mechanism (Sanderson *et al.* 2015c; Khera *et al.* 2021).

There are typically two ways by which individuals leave their natal group. The first is through eviction whereby a group of individuals are forced to leave as a result of aggression displayed by other group members (Cant *et al.* 2001). The second is when a cohort of individuals of the same sex (usually males) choose to leave the group of their own accord when they encounter another cohort of individuals consisting of the opposite sex, upon which they establish a new group (Cant *et al.* 2001). Forced evictions are generally thought to be the result of the high level of within-group reproductive competition as reproductive success per breeding female is negatively associated with the number of breeding females (Cant *et al.* 2010).

1.3.5 Cooperative breeding in banded mongooses

Within banded mongoose social groups, pups receive two main forms of help from adult group-members: babysitting and escorting (Fig 2). After birth, communal litters are guarded from predators and rival groups by one or more adult 'babysitters' who remain at the den whilst the rest of the group forages. All adult group-members (over 6 months) regardless of sex, social status or age usually contribute to babysitting the pups for at least one foraging session, regardless of relatedness to the litter (Vitikainen *et al.* 2017). Babysitting has been shown to increase the likelihood of pup survival, with the number of babysitters present being positively associated with the likelihood of survival to emergence, though surprisingly the number of individuals that stay behind to babysit was not found to increase with group size (Cant 2003). This could be a form of load lightening with the cost of guarding pups being spread over multiple helpers.

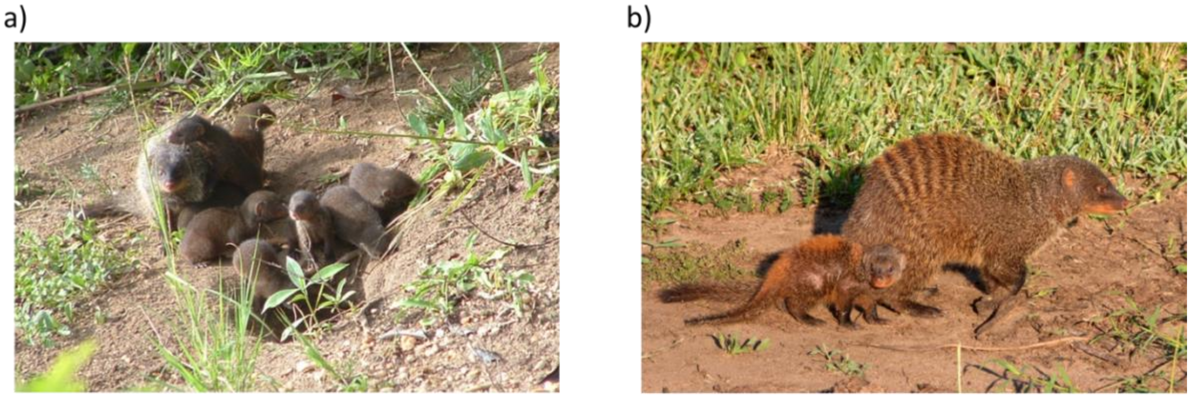


Figure 2. Banded mongoose engaging in a) babysitting and b) escorting behaviour (Nichols *et al.* 2021)

Pups are babysat until they emerge from their dens (at ~30 days), after which they start accompanying the rest of the group on foraging trips (Cant *et al.* 2013). At this point, most pups form a one-to-one relationship with an adult helper, known as an 'escort' that provides the pup with food and protection until the pups reach nutritional independence at ~90 days (Cant *et al.* 2013), though many pups (43%) that emerge die before reaching independence, most likely due primarily to predation (Hodge 2005). Adults vary in the amount of escorting care they provide, and many adults do not escort a pup (Nichols *et al.* 2021). Similar to babysitting, escorting has been shown to increase pup survival to nutritional independence, and pups that receive more care are found to be heavier at one year of age (Vitikainen *et al.* 2019).

Both forms of helping are costly behaviours with babysitting requiring one or more individuals to forgo foraging in order to stay behind and look after the communal litter (Cant 2003). This can last for up to nine hours, though babysitting sessions more commonly last on average 4.5 hours in the morning and two hours in the afternoon (Cant 2003). Helping results in weight loss for babysitters

(Hodge 2007; Cant *et al.* 2016) and escorts that invest more with regards to feeding pups gain weight at a lower rate (Hodge 2007). As a result, when rainfall, and resultantly food availability is low, non-breeding individuals contribute less to helping (Nichols *et al.* 2012a). Since banded mongooses live in tight-knit family groups where members are usually highly related to one another (Nichols *et al.* 2012c), helpers gain indirect fitness benefit from 'helping' dominant breeders raise their litters. Furthermore, breeders also contribute to pup care and so gain direct fitness benefits (Cant 2003). This is sets banded mongooses apart from most other cooperative breeders, as we see both communal breeding (where several individuals breed together and take care of pups communally) and cooperative breeding (where non-breeding helpers provide care) taking place. This is due to the low reproductive skew in banded mongooses, whereby there is more than one dominant breeder within a group (Cant 2000).

Individuals were recorded as babysitting if they were observed at the den during a foraging session or if they were absent from the foraging group provided the group was more than 100m from the den and the group was visited for more than 15 mins (Cant 2003; Nichols *et al.* 2012a). This distance was used because individuals of a group foraging together were never more than 100m apart (Cant 2003; Nichols *et al.* 2012a). Individuals were recorded as escorting if they were within 30cm of a particular pup for over 50% of a 20-minute observation period (Gilchrist *et al.* 2004; Sanderson *et al.* 2015b). Behavioural data used in this study includes babysitting data collected since February 2000, which incorporates 17,342 babysitting events from 555 unique communal litters. We also used escorting data collected since June 2000, incorporating 13,692 observations of escorting for 1000 pups from 213 individual litters.

1.3.6 Environmental conditions

The climate in Uganda can be characterised by two 'wet' seasons per year, which are characterised by heavy and frequent rainfall (Fig 3). The first wet season from March to May is shorter and more intense, whilst the second wet season from August to December is longer and wetter overall (Marshall *et al.* 2016). During wet seasons, there are changes in vegetation and invertebrate abundance, increasing the food availability for banded mongooses (Cant *et al.* 2013; Marshall *et al.* 2017). There is however a small delay in the time it takes for high rainfall to translate into high invertebrate abundance (Marshall *et al.* 2017). Between these wet seasons are two short dry seasons from January to February and June to July (Fig 3). The temperature in Uganda stays relatively constant year-round, as expected from an equatorial region (mean of monthly mean maximum daily temperature at our study site ± standard deviation [SD] = 29.5 ± 1.5 °C) (Marshall *et* *al.* 2016)). Whilst Uganda is generally considered aseasonal with regards to temperature, January-February are normally the hottest months of the year (Fig 3).

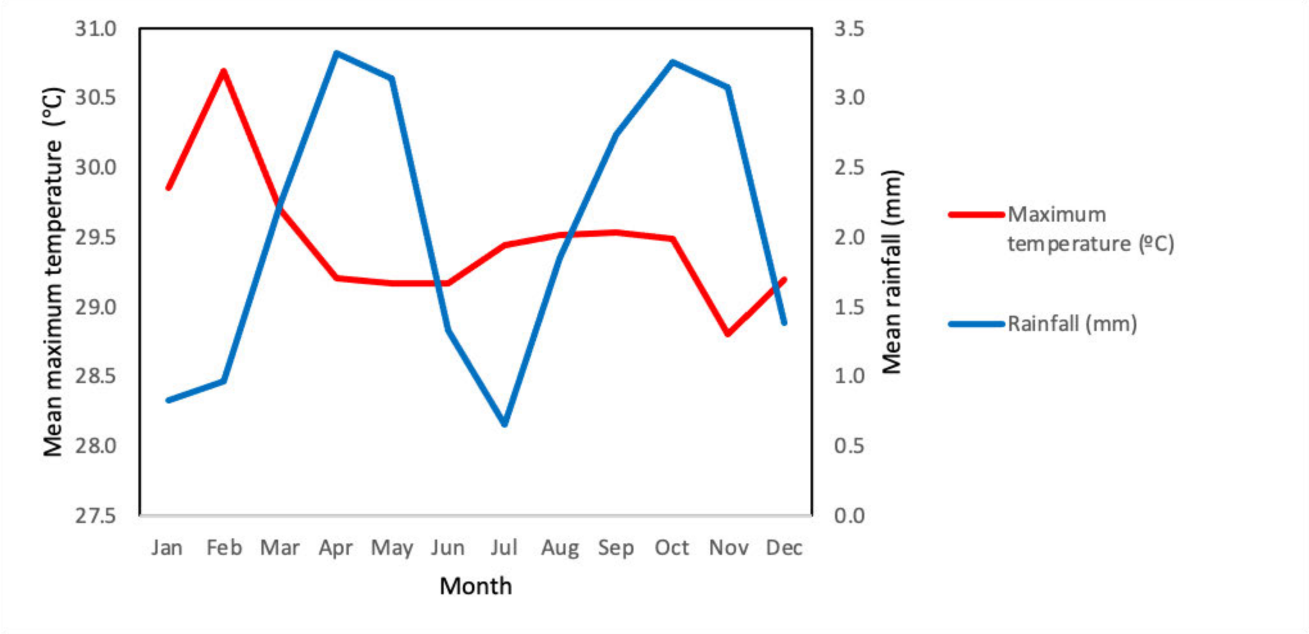


Figure 3. The monthly mean daily rainfall (mm) (blue line) and monthly mean maximum daily temperature (°C) (red line) in Mweya, Uganda between April 1999 to June 2020.

1.4 Thesis aims and structure

This thesis aims to investigate how seasonal, long-term, and short-term changes in climatic conditions affects banded mongoose reproduction, early life survival, body condition and behaviour.

Chapter 2 decomposes climate data (rainfall and temperature) into short-term, seasonal, and long-term changes and investigates their impacts on the fecundity of our banded mongoose population, (focusing on pregnancy and birth rates, along with the number of foetuses carried by pregnant females). I also investigate the effect of group size and whether/how the effect of climate varies with different group sizes.

Chapter 3 investigates how survival to emergence and nutritional independence are affected both directly and indirectly (through effects on helping behaviour) by short-term, seasonal, and long-term changes in rainfall and temperature. I also investigate whether large groups can buffer against harsh conditions. To investigate both direct and indirect effects under one framework I use Structural Equation Modelling (SEM's) to investigate causal pathways.

Chapter 4 investigates the impact of high temperatures on pup weight at emergence from the den. Specifically, I test the Heat Dissipation Limit (HDL) theory, which predicts that mothers are forced to suppress lactation under hot conditions, leading to reductions in pup growth.

Chapter 5 involved conducting focal observations on banded mongooses at the field site to investigate 1) whether individuals are able to behaviourally thermoregulate under hot conditions by reducing activity levels and foraging time, and 2) whether this is sufficient to prevent body surface temperatures from increasing at high temperatures and high humidity. Understanding behavioural thermoregulation, in particular its impact on foraging, aids with interpretation of findings from the long-term data.

Chapter 6 summarises and ties together my key findings from each study in order to provide a broader picture of how climate affects banded mongoose survival and behaviour, and how these findings may apply more broadly to equatorial species.

2 Banded mongoose reproduction is driven by environmental variation across multiple time-scales

2.1 Introduction

Choosing when to reproduce is an important life history decision, which impacts individual fitness and has consequences for the survival of a population over time (Milligan & Lloyd 2009). Reproduction is also energetically costly and so under poor environmental conditions, when food is scarce, reproduction may be delayed until conditions improve (Bronson 2009). This leads to many populations reproducing seasonally, at a time of year when conditions are most favourable (Bronson 2009). Indeed, reproduction is found to be strongly linked to environmental conditions in a variety of mammalian species (Bronson 1985) from bats (Lučan *et al.* 2013) to bears (Spady *et al.* 2007).

In temperate climates, reproductive rates are generally higher during spring and summer months where high air temperatures positively affect food availability compared to the winter months where food availability is low (Wingfield *et al.* 1992; McNutt *et al.* 2019). Whilst these seasonal changes in environmental conditions are usually quite reliable in temperate climates, favourable conditions for reproduction (such as weather conditions and food availability) are generally less predictable at lower latitudes (Bronson 1985; Wingfield *et al.* 1992; Brown & Shine 2006). The seasonality of the tropics has often been overlooked due to mean monthly temperatures being relatively constant compared to temperate latitudes (Janzen 1967; Abernethy *et al.* 2018). However, tropical climates are typically characterised by marked “wet” and “dry” seasons. So, whilst in temperate regions the timing of reproduction is strongly linked to temperature, in lower latitudes rainfall can become more important (Cohen *et al.* 2018). This presents a greater challenge for tropical species since they must time their reproduction in accordance with rainfall, which is comparatively less predictable both temporally and spatially than temperature (Shine & Brown 2008). Consistent with this, previous studies on tropical animal populations, including those on rodents (Bergallo & Magnusson 1999) and bats (Zortéa 2003), have found that reproduction is often timed to coincide with the wet season because higher rainfall tends to increase food availability. Whilst most previous studies on reproduction have focused on temperature-based seasons, rain-based seasons have been comparatively understudied (Varpe 2017).

Although many animal populations are adapted to regular and expected seasonal changes in their external environment (Brogi *et al.* 2022), human-induced global climate change has disrupted reproduction. For instance, multiple bird species have started migrating to breeding grounds earlier in the year (Cotton 2003; Mills 2005; Sparks *et al.* 2005) and reproductive success has declined in numerous species including Magellanic penguins (*Spheniscus magellanicus*) (Boersma & Rebstock 2014), northern muriquis (*Brachyteles hypoxanthus*), (Wiederholt & Post 2011) and baboons (*Papio cynocephalus*) (Beehner *et al.* 2006). Whilst some species such as red deer (*Cervus elaphus*) have been shown to adapt their reproductive timing to match this change in climate (Moyes *et al.* 2011), other species such as roe deer (*Capreolus capreolus*) have continued to give birth at the same time despite the earlier onset of spring (Plard *et al.* 2014). This has resulted in a temporal mismatch between the seasonal peak in births and optimum foraging conditions, with negative consequences for offspring fitness and early life survival, both at the individual and population level (Plard *et al.* 2014).

The impact of climate change on reproduction in tropical animal populations is arguably more difficult to predict compared to those in temperate regions since reproduction is generally more affected by rainfall (Shine & Brown 2008) and the effect of climate change on rainfall also appears to vary between regions (Hendrix & Salehyan 2012; Feng *et al.* 2013). Furthermore, whilst the impact of climate change on species living in mid-high latitudes has been extensively studied, the impact on equatorial species has been comparatively understudied (Feeley & Silman 2011). Long term studies on tropical populations are vital to our understanding of these questions, but are challenging due to the lack of resources allocated to conducting scientific research in these regions, and to long-term studies of wild populations generally (Abernethy *et al.* 2018). Many previous studies on tropical species have also assumed that because there is little year-round variation in temperature, it is biologically unimportant. However, since tropical species generally have narrow thermal ranges, they could be disproportionately sensitive to even small temperature changes (Tewksbury *et al.* 2008; Bozinovic 2011). Tropical species may therefore be particularly vulnerable to rapid climate change, compared to temperate species which are used to greater fluctuations in temperature (Şekercioğlu *et al.* 2012). The heat dissipation limit theory suggests that reproductive output in endotherms should be constrained by their ability to dissipate body heat resulting in reproduction being negatively affected by high temperatures (Speakman and Król 2010). Some support for this theory has been provided by studies conducted on tropical mammals, for example, increasing long-term temperatures have continually delayed parturition, and higher denning temperatures have reduced litter size in wild dogs (*Lycaon pictus*) (Abrahms *et al.* 2022). There are however, few other studies that have investigating the impact of raising temperatures on tropical species.

In addition to the impact of long-term and seasonal changes in environmental conditions, short-term fluctuations including extreme weather events can also have significant impacts on reproduction and are expected to become more frequent as climate change continues (IPCC 2012). For example, in Argentina, not only has the higher variability in climate lowered reproductive success in Magellanic penguins (*Spheniscus magellanicus*), but as the intensity and frequency of storms continues to increase so does the likelihood of reproductive failure (Boersma & Rebstock 2014). Similarly, following periods of droughts, female baboons (*Papio cynocephalus*) are less likely to enter reproductive cycles, are less likely to conceive and are less likely to carry pregnancies to term (Beehner *et al.* 2006). Sudden heat-waves can also cause individuals to suffer from heat stress which can disrupt reproduction (Takahashi 2012). Individuals suffering from heat stress may reduce their food intake to slow down their metabolism and therefore reduce heat production in the body; this can impact both energy balance and nutrient availability, both of which can affect pregnancies (Hansen 2009). Finally, high short-term temperatures have also been shown to affect human reproduction with high temperatures during the first few weeks of conception increasing the risk of pregnancy loss (Hajdu & Hajdu 2021). Hence, impacts of changing climates may operate through both long-term and short-term changes, and disentangling these scale-dependent effects in natural systems requires long-term life history data on wild populations.

Our 20-year study on banded mongooses (*Mungos mungo*) in Uganda presents an exceptional opportunity to advance our understanding of the impacts of short and long term changes in environmental conditions on reproduction. First, this population has experienced variation in both rainfall and temperature over different timescales. As is typical of the tropics, the climate in Uganda is characterised by two wet seasons per year: a short-wet season from March-May and a longer-wet season from August-December, with little seasonal variation in temperature (Marshall *et al.* 2016). Our study population also experiences short term fluctuations in conditions, with some months being wetter, drier, hotter or cooler than average for the time of year. Environmental conditions in Uganda are also changing over longer time periods; across western Uganda, rainfall has on average increased between 1983 and 2016, with increases in both the total amount of rainfall and the duration of wet seasons, although with considerable between-year variation (Diem *et al.* 2019b, a). The average temperature in southwest Uganda has also increased by an average of 0.3°C each decade since the 1960's (GoU 2007), and temperatures are predicted to continue to rise in western Uganda and more broadly across the Great African Lakes region by 1-2°C by 2050 (Babel & Turyatunga 2015; Asefi-Najafabady *et al.* 2018).

Second, we have collected extensive data on reproduction in our study population, allowing us to investigate the impact of variation in environmental conditions on all stages of pregnancy, from conception to birth. Banded mongooses live in social groups of approximately 10-30 adults, which reproduce up to four times per year and can give birth in any month (although births are not equally spread over months). Reproduction is synchronised within (but not between) groups (Hodge *et al.* 2011; Cant *et al.* 2016). Female group-members enter oestrus within a few days of each other, after which a mean of 83% of adult females become pregnant, carrying up to five pups each (mean ± SD = 2.84 ± 0.12) (Cant 2000). Not all pregnancies are carried to term, with at least 43% of pregnancies being lost before birth (Inzani *et al.* 2019). Females give birth in close synchrony (usually on the same day) (Hodge *et al.* 2011) and the resultant litters are then raised communally with input from most group-members (Cant 2003).

Rainfall is likely to impact on reproduction through its effect on invertebrate abundance; with higher levels of rainfall increasing the abundance of prey species (Cant *et al.* 2013; Marshall *et al.* 2017). Previous studies on banded mongooses have investigated the impact of rainfall over different time periods on banded mongoose fecundity and have found inconsistent results. Gilchrist et al (2004) found no impact of rainfall over the past 5 months on conception probability, abortion probability, foetus count, or inter-conception interval, but there was a significant impact on age at first conception. Similarly, Cant (2000) found no significant effect of rainfall during the month of oestrus, nor during the month in which females gave birth, on the proportion of females in the group becoming pregnant, and Marshall et al (2017) found no impact of mean or variation in rainfall over the first year of life on female body condition, lifespan, or lifetime reproductive success (although there were significant impacts on males). However, Nichols et al (2012) found that rainfall over the 60 days of gestation impacted the breeding success of low-ranking, but not high-ranking, females. This was because, when rainfall was low and within-group competition for resources was high, low-ranking females were violently evicted from their social groups, leading to them aborting their litters (Nichols *et al.* 2012b; Inzani *et al.* 2019). However, we do not know whether these impacts are related to seasonal changes in rainfall, longer-term climatic trends, or short-term weather events such as droughts, making it unclear what the impacts of climate change may be on banded mongoose reproduction. Furthermore, no study has yet investigated the impact of temperature on fecundity in banded mongooses.

Here, we decompose variation in both rainfall and temperature into short-term, seasonal, and long-term trends, and investigate their impact on female fecundity (pregnancy, birth and number of foetuses carried). We predict that females time reproduction according to predictable seasonal changes in rainfall. As high rainfall leads faster pup growth (Bell *et al.* 2012), females may benefit from timing their births to coincide with rainy seasons, whereby food will be most abundant for growing pups. We also predict that, due to impacting food supply, reductions in rainfall over long periods will lead to declines in birth (but not necessarily pregnancy) rates and foetus numbers, because unseasonably low rainfall may lead to increased likelihood of foetuses being aborted. High short and long-term temperatures could cause heat stress in females, which may reduce fecundity, in which case birth rates and foetus counts may be lower when temperatures are high. On the other hand, as temperatures are highest shortly before the onset of the rainy seasons, seasonally high temperatures may be associated with higher pregnancy rates. Finally, we use our results to evaluate the potential impacts of climate change on the fecundity of our study population.

2.2 Methods

2.2.1 Study system and data collection

We used behavioural, life history and environmental data collected from a population of wild banded mongooses residing in Mweya, Queen Elizabeth National Park, Uganda (0° 12’S, 27°54’E) collected between June 2000 and July 2020. At any one time, the population consisted of approximately 250 individuals, living in 10-12 groups. Our study population was habituated to observation at <10m (usually <5m) and was visited every 1-3 days to determine group composition, monitor pregnancies and determine birth dates. Pregnant females were identified at around 40 days into their pregnancy due to weight gain and the visible swelling of their abdomen; in many cases, this was confirmed by ultrasound scans and palpitation of the abdomen (Cant 2000; Gilchrist 2006a; Inzani *et al.* 2019). Births usually occurred at around 60 days after conception and were identified based on the absence of the previously pregnant females on foraging trips the morning after birth, the start of pup-care behaviour, and abdomen size returning to normal (Gilchrist 2006a; Hodge *et al.* 2011). We defined group size as the number of individuals over 6 months old present in the group at the relevant time point (Cant 2003; Gilchrist *et al.* 2004).

2.2.2 Decomposition of environmental variables

To quantify environmental variation, we used rainfall (mm) and maximum temperature (°C) data collected from Mweya meteorological station, at the centre of our study site. When modelling our environmental variables, we differentiated between short-term environmental fluctuation, seasonal variation and long-term trends. To do this, we decomposed both temperature and rainfall data into three components using the decompose function in R version 4.2.1 (R Core Team 2022): (1) seasonal variation representing consistent intra-annual change (2) long-term trends, and (3) short-term environmental fluctuations representing irregular changes in the environment. To do this, we calculated monthly averages and subsequently formatted our data as a time series, which was then decomposed into seasonal variation and short-term environmental fluctuations. The decompose function estimates long-term changes using moving averages, then extracts the seasonal component by calculating the average value for each month across all years. Short-term variation was defined as the residual variation left over from the time series once the long-term and seasonal components are removed (Fig 1). Over the 20-year period of our study, for logistical reasons it was not always possible to collect daily environmental data (e.g. due to staff sickness or time constraints), resulting in a small proportion of missing values: 524 days (6.75%) for maximum temperature and 421 days (5.42%) for rainfall. We imputed missing values with estimated values using the imputeTS package (Moritz & Bartz-Beielstein 2017) prior to the time series decomposition. The decomposed environmental variables were used as fixed effects in our subsequent statistical models.

2.2.3 Statistical analyses

We used generalized linear mixed effects models (GLMMs) implemented using the R package lme4 (Bates *et al.* 2015) in R version 4.2.1 (R Core Team 2022) to investigate the effects of environmental variables on all stages of pregnancy. We constructed three groups of models, each with a different fecundity-related response variable; (1) the total number of pregnancies per social group per month (2) the total number of births per social group per month and (3) the number of foetuses carried by females. Because groups with more adult females have a greater reproductive potential within a given month, we also investigated the proportion of females in each group that were recorded as pregnant or gave birth. However, the proportional results differed little from the total number results, so are presented in the supplementary material. Our environmental variables were fitted as explanatory variables, alongside group size and group size squared to account for linear and non-linear impacts related to group size, such intra- and inter-group competition for resources. As group size has previously been shown to interact with environmental conditions to impact on reproduction (Nichols *et al.* 2012b), we tested for such interactions in our models. All continuous explanatory variables were scaled so that main effects could be interpreted in the presence of interactions (Schielzeth 2010). We fitted group identity as a random effect (unless this resulted in a variance of zero) as multiple observations were taken from the same social group. In order to deal with cases of overdispersion in our proportion (binomial) models, we included an Observation Level Random Effect (OLRE), giving each observation a unique level of random effect (Harrison 2015). We used a negative binomial distribution to correct for overdispersion when investigating the total number of pregnancies and births. The 'BOBYQA' optimizer algorithm was used in our pregnancy and birth models in order to deal with convergence problems (Bates *et al.* 2015). As it may take time for rainfall to alter invertebrate abundance, we also compared models incorporating zero, 1-month and 2-month lags in the effect of rainfall.

Attempting to model all six potential interactions between environmental variables and group size plus the six potential interactions between group size squared (to account for non-linear effects) and environmental variables as well as main effects in one model led to a singular fit. Therefore, to avoid fitting an overly complex model, we took a model comparison approach, comparing biologically plausible models alongside null (group size-only) models using Akaike Information Criterion (AIC) and selecting the best fitting model (Johnson & Omland 2004; Arbuckle & Minter 2015; Matuschek *et al.* 2017). Standard model checks were employed following Crawley (2015). We used prior knowledge of banded mongoose biology to construct biologically realistic models in three stages.

Stage 1: We started off by constructing models with seasonal environmental variables, which are likely to be important as banded mongoose breeding shows peaks during the rainy seasons. We started with a null model where the response variable was only modelled as a function of group size. This null model was used as a base to create four other models that incorporated seasonal fluctuations. The first model (S1) included seasonal rain (plus interactions between group size and seasonal rain); the second model (S2) included seasonal temperature (plus interactions between group size and seasonal temperature); the third model (S3) included seasonal rain and seasonal temperature (along with the interactions between the seasonal variables and group size); the fourth model (S4) was the same as the third model with the addition of an interaction term between seasonal rain and seasonal temperature. If interactions between group size and environmental variables were nonsignificant for all four of the models, then these interactions were removed from the models; if group size on its own was also non-significant in all four models, then this was removed as well. These five models (including the null model) were then compared using AIC. During our model selection process, we chose the model with the lowest AIC value unless there was a less complicated model with an AIC value within two points of the best model. The best of these five models was then moved forward to the next stage where it was used as a base for investigating the potential effects of short-term fluctuations in environmental variables.

Stage 2: Following the same pattern as the previous set of models, the first model (R1) included short-term variation in rainfall (along with interactions between group size and short-term variation in rainfall); the second model (R2) included short-term variation in temperature (along with interactions between group size and short-term variation in temperature); the third model (R3) included both short-term variation in rainfall and temperature (along with interactions with group size); the fourth model (R4) was the same as the third model with the addition of an interaction between short-term variation in temperature and rainfall. If interactions between group size and environmental variables were non-significant for all four of the models, then these interactions were removed from the models; if group size on its own was also non-significant in all four models, then this was removed as well.

Stage 3: The best model from Stage 2 was then used as a base for modelling the potential effects of long-term trends in rainfall and temperature; this followed the same procedure as before (models T1, T2, T3, and T4). Model comparison tables are available in the supplementary information (Table S1, S2, S4, S5). Further details of our models are described below.

2.2.4 Pregnancy rates

Between 2000 and 2019, we made 1641 monthly observations covering 21 social groups, with 498 of those observations (30.3%) finding at least one female in the group to be pregnant. To model the number of pregnant females (per group per month) we used GLMMs with group identity fitted as a random effect. In order to correct for overdispersion ($\theta = 1.67$), we used a negative binomial distribution. When modelling the proportion of females within a group that were pregnant, we corrected for overdispersion ($\theta = 1.93$) by adding an OLRE. Since adding group identify as a random effect explained zero variation, we did not include this in the proportion models.

2.2.5 Parturition rates

Between 2000 and 2019, we made 1861 monthly observations covering 24 social groups, with 677 of those observations (36.4%) finding at least one female in the group to have given birth. To model the number of females that gave birth (per group per month) we used GLMMs with group identity fitted as a random effect. In order to correct for overdispersion ($\theta = 2.79$) we used a negative binomial distribution. When modelling the proportion of females within a group that gave birth an OLRE was added to correct for overdispersion ($\theta = 1.93$) and since adding group identify as a random effect explained zero variation, we did not include this in the proportion models.

2.2.6 Number of foetuses

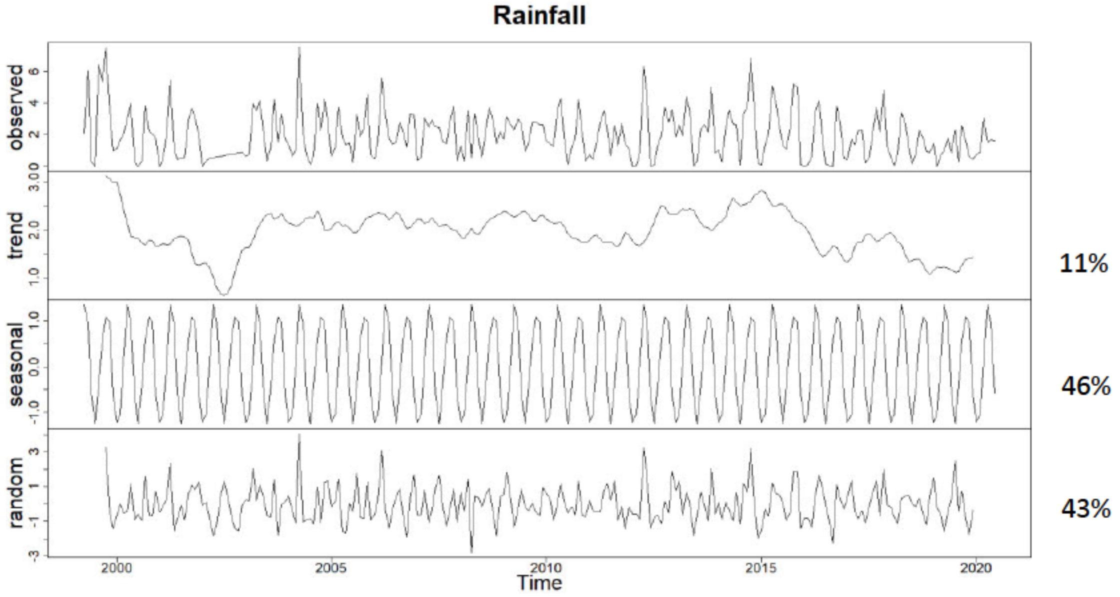
Between 2009-2013 we used 229 ultrasound scans from 93 pregnant females covering 9 social groups to determine the effects of environmental conditions and group size (plus potential interactions) on the number of foetuses produced by pregnant females. When ultrasounds were taken, there was uncertainty in 9 observations (3.9%) concerning the number of foetuses present and, in these cases, ranges were given instead. If this occurred, we took the midpoint and rounded down to the nearest whole number. We modelled the number of foetuses using GLMMs with group identity and the female from which the scans were taken fitted as a random effect since scans were sometimes taken from the same individual during different pregnancies. We found that the data was underdispersed ($\theta = 0.209$) which can result in standard errors being overestimated and biased inferences (Forthmann & Doebler 2021). We therefore used a Conway-Maxwell-Poisson distribution from the glmmTMB package (Brooks *et al.* 2017) which accounts for underdispersion (Shmueli *et al.* 2005).

2.3 Results

2.3.1 Decomposition of environmental variables

Rainfall varied considerably over time, ranging from an average of 0 to 7.51 mm per day over each month. Our decompositions showed that seasonal variation explained a large percentage of variance (46%) in the observed average monthly rainfall (Fig 1a); with two distinct peaks in seasonal rainfall per year, one lower but longer lasting (the long-wet season) and another higher but short lived (the short-wet season) (Fig 1a). Long-term changes explained relatively little variance (11%) in rainfall, while short-term changes explained 43% of variance, demonstrating that rainfall often fluctuates over short timescales.

Temperatures remained relatively constant over time, with our observed average monthly maximum temperatures varying from 25.68 to 34.26 °C. Seasonal variation in temperature was lower than for rainfall, explaining 21% of variance (Fig 1b). Long-term changes explained almost half (48%) of the variation in the observed monthly maximum temperature while short-term changes explained 31% of the variance in temperature (Fig 1b).



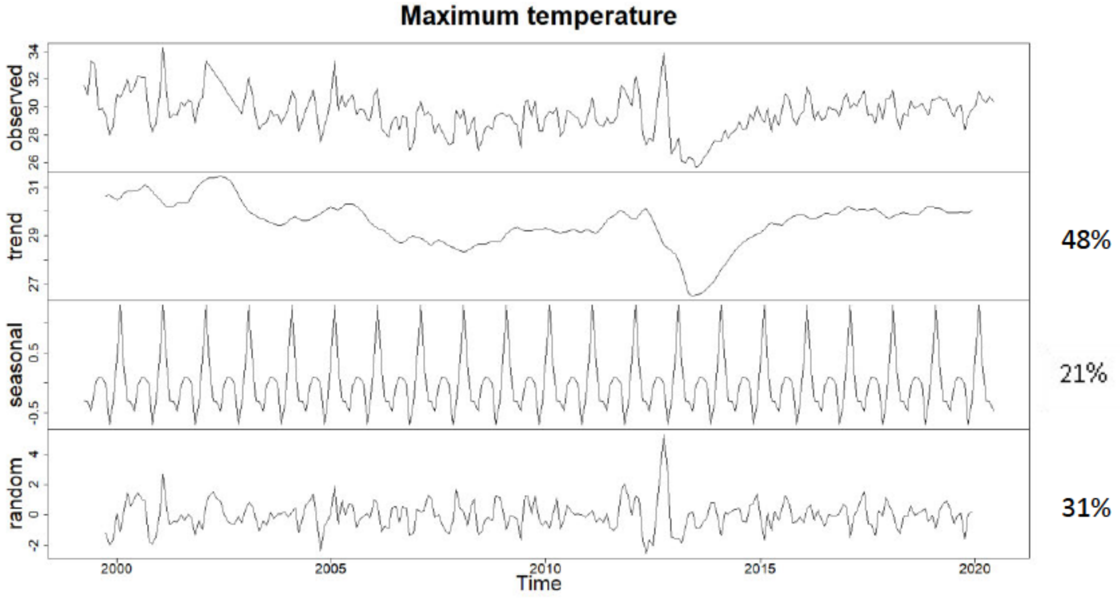


Figure 1. Decomposition output from the mean daily (a) rainfall (mm) and (b) maximum temperature (°C) per month from October 1999 to December 2019 including the long-term changes, seasonal fluctuation, and short-term variation, along with the percent of variance explained by each component. All the components are in the original scale with the exception of seasonality which has been mean-centered by subtracting the average seasonal value from each data point.

2.3.2 Pregnancy rates

We found a strong degree of seasonality in pregnancy rates, with more pregnancies occurring in warmer and wetter seasons (Table. 1, Table S3, Fig. 2a, Fig. 2b, Fig. S1a, Fig. S1b). We also found a lag in the impact of environmental variables, with temperature and rainfall in the previous month having the strongest effect on pregnancy. Short- and long-term variation in environmental variables did not improve the model fit so were not included in the final model. Intermediate-sized groups had the largest number of pregnant females (estimate = -0.174 ± 0.054, z-statistic = -3.20, p=0.00138) (Table. 1, Fig. 2c). This is probably because small groups contain few females, whilst large groups show greater levels of reproductive competition (Cant *et al.* 2001; Gilchrist 2006b). Consistent with this, the proportion of pregnant females decreased with increasing group-size (Table. S3, Fig. S1c).

Table 1. The number of pregnant females per group per month as a function of group size and environmental conditions in the previous month.

Fixed effects	**Estimate**	**SE**	**z-value**	**p-value**
(intercept)	0.128	0.099	1.29	
Group size	0.027	0.073	0.365	0.715
Group size^2	-0.174	0.054	-3.2	0.00138
Maximum seasonal temperature (in the previous month)	0.301	0.067	4.51	6.48×10^{-6}
Seasonal rainfall (in the previous month)	0.257	0.068	3.8	1.45×10^{-4}

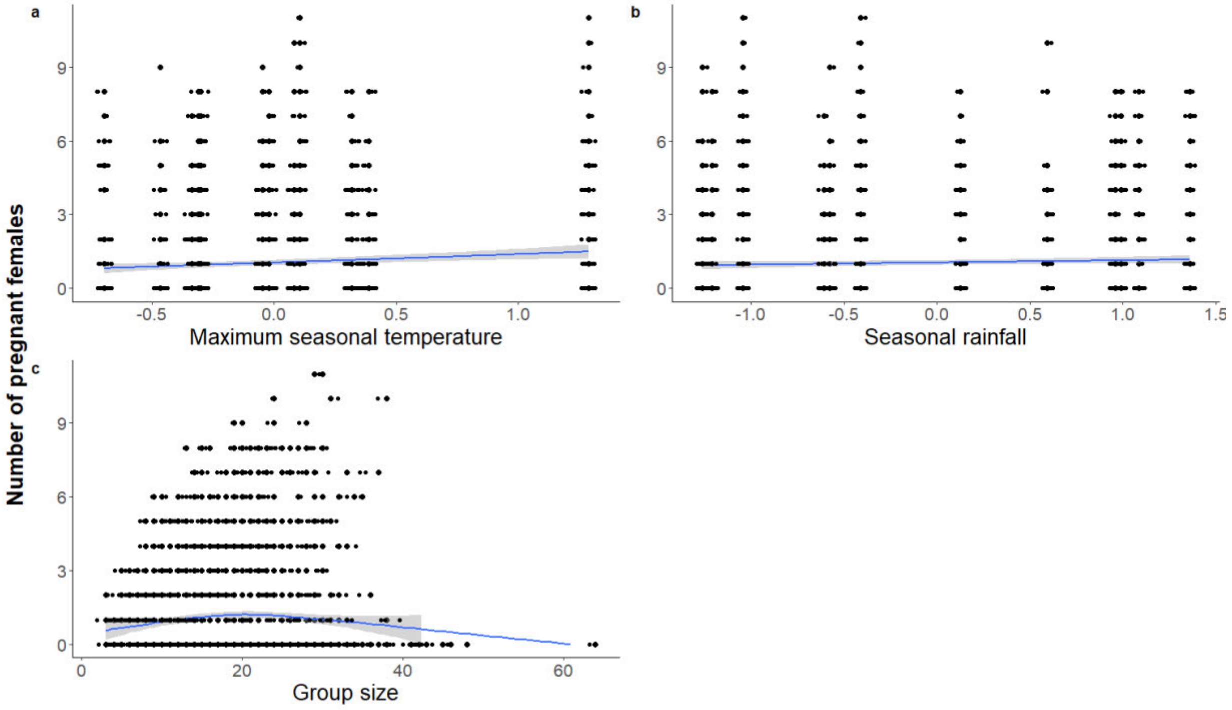


Figure 2. The number of pregnant females per group per month as a function of a) maximum seasonal temperatures in the previous month, b) seasonal rainfall in the previous month and c) group size.

2.3.3 Parturition rates

Parturition rates were higher during wet seasons, but did not vary with seasonal temperature (Table. 2, Table. S6, Fig. 3b, Fig. S2a). We also found a significant interaction between variation in long-term temperature and rainfall; the number of females giving birth was higher during hot and wet conditions but lower during hot and dry conditions (estimate = 0.112 ± 0.051 z-statistic = 2.21, p=0.027) (Table. 2, Fig. 3a). As with pregnancy rates, there was a one-month lag in the impact of environmental conditions. Additionally, we found that more females gave birth in larger groups (estimate = 0.323 ± 0.058, z-statistic = 5.60, p=2.12x10^{-8}) (Fig. 3c). This is likely due to there being more females in larger groups, as the proportion of females giving birth did not vary with group size (Table. S6). Finally, while short-term temperatures had no impact on the number of females giving birth, the proportion of females giving birth was lower at high short-term temperatures (estimate = -0.239 ± 0.109, z-statistic = -2.20, p=0.0276) (Table. S6, Fig. S2b).

Table 2. The number of females giving birth per group per month as a function of group size and environmental conditions in the previous month (including interactions).

Fixed effects	**Estimate**	**SE**	**z-value**	**P-value**
(intercept)	0.257	0.0782	3.24	
Group size	0.323	0.0577	5.6	2.12×10^{-8}
Group size^2	-0.118	0.0385	-3.13	2.25×10^{-3}
Seasonal rainfall (in the previous month)	0.323	0.0501	6.445	1.15×10^{-10}
Maximum trend temperature (in the previous month)	0.0466	0.0574	0.812	0.417
Trend rainfall (in the previous month)	0.0599	0.0639	0.937	0.349
Maximum trend temperature (in the previous month): Trend rainfall (in the previous month)	0.112	0.0507	2.21	0.0269

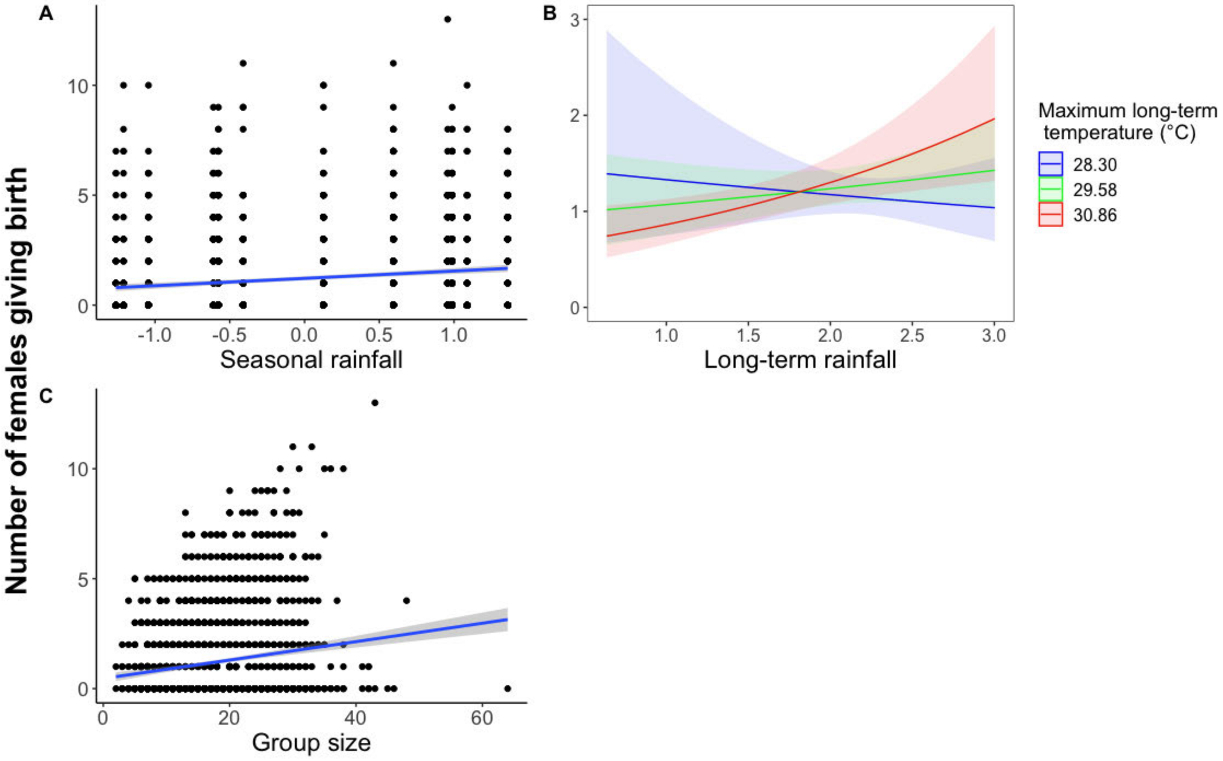


Figure 3. The number of females giving birth per group per month as a function of a) seasonal rainfall in the previous month, b) the interaction between long-term rainfall and temperature in the previous month and c) group size.

Table 3. The number of foetuses present within pregnant females as a function of group size and environmental conditions (including interaction effects).

Fixed effects	Estimate	SE	z-value	p-value
(intercept)	1.052	0.034	30.7	
Maximum seasonal temperature	0.069	0.021	3.31	9.23×10^{-4}
Maximum random temperature	0.031	0.022	1.37	0.17
Group size	-0.015	0.032	-0.481	0.63
Maximum trend temperature	0.021	0.022	0.95	0.342
Maximum random temperature: Group size	0.063	0.025	2.53	0.0116
Group size: Maximum trend temperature	0.127	0.038	3.37	7.66×10^{-4}

Number of foetuses

We found no association between rainfall and foetus number, but seasonal, short- and long- term variation in temperature had significant effects. Pregnant females carried more foetuses during warmer seasons (estimate = 0.069 ± 0.021, z-statistic = 3.31, p-value = 9.23×10^{-4}) (Fig. 4c, Table. 3). Short- and long-term temperatures interacted with group size to predict foetus number. At low short-term temperatures, females in small and medium groups carried more foetuses than females in larger groups, but females in larger groups carried similar or greater numbers of foetuses at higher short-term temperatures (estimate = 0.063 ± 0.025, z-statistic = 2.53, p=0.0116) (Fig. 4a, Table. 3). Foetus number was unaffected by long-term trends in temperature in medium and large groups but females in small groups carried fewer foetuses as temperatures increased (estimate = 0.127 ± 0.038, z-statistic = 3.37, p=7.66×10^{-4}) (Fig. 4b, Table. 3). As with the other fecundity-related variables, there was a one-month lag in the effect of environmental conditions.

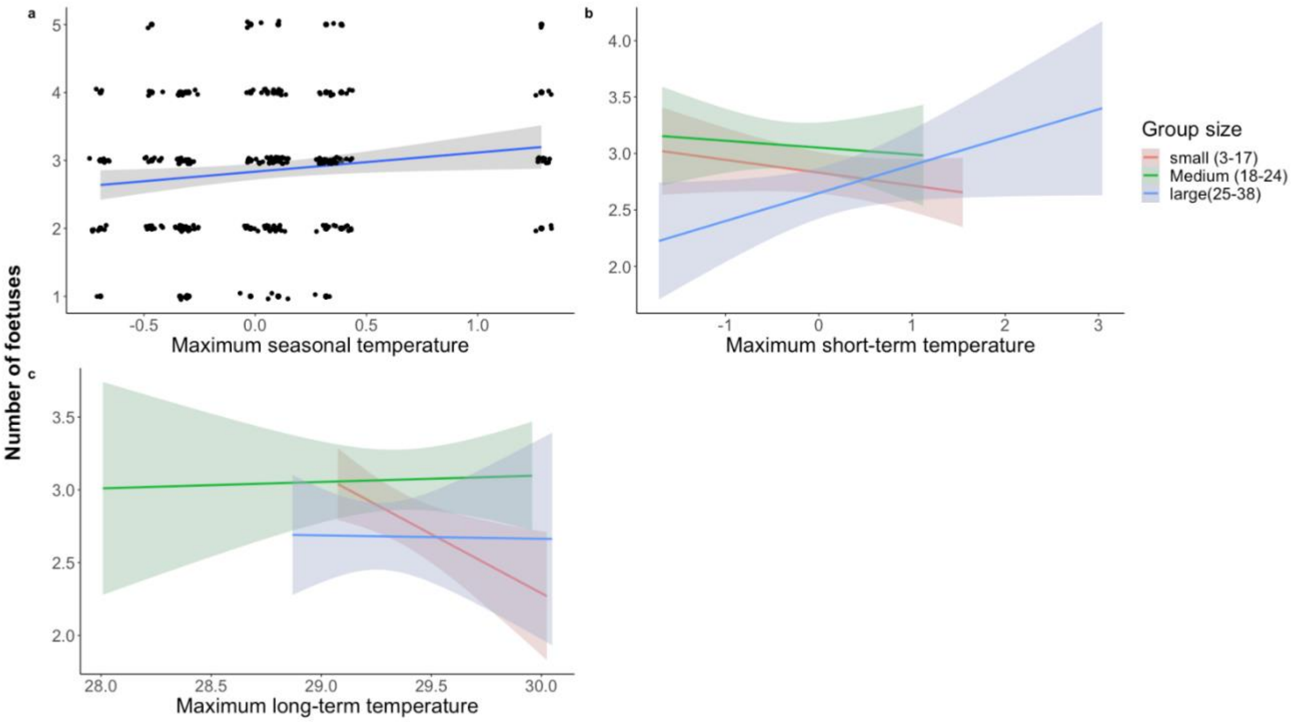


Figure 4. The number of foetuses identified within pregnant females during ultrasound scans as a function of a) the maximum temperature, b) the interaction between group size and maximum short-term temperature and finally c) the interaction between group size and maximum long-term temperature. The graphs shows the regression lines from the raw data.

2.4 Discussion

2.4.1 Fecundity varies with seasonal changes in rainfall and temperature

Our study found seasonal effects on fecundity, with females being both more likely to be pregnant and to give birth during wet seasons, confirming previous anecdotal evidence of higher levels of reproduction during wet seasons. In dry seasons, 11.07% of females within groups were pregnant with 12.88% giving birth, and during rainy seasons, 19.93% of females were pregnant with 21.21% giving birth. Timing reproduction to coincide with the wet season is likely to be highly advantageous since higher seasonal rain increases both pup survival to emergence (Chapter 3) and pup weight (Nichols *et al.* 2012b), in turn boosting pup survival to nutritional independence (90 days) (Nichols *et al.* 2012b). Due to the advantages for pups of being born during the wet season, we predicted that births would be timed to coincide with high seasonal rainfall, and our results are in accordance with this prediction.

However, pregnancies last 59-63 days (IQR=3.5-4) (Cant 2000), and pups are dependent on lactation for a further 30 days and are not nutritionally independent until they are 90 days old, so it is not possible for a female to carry a pregnancy, give birth and raise the resultant litter over the course of a single wet season (which last approximately 90 days). Therefore, females that are pregnant a month after the peak of a wet season are likely to be raising their pups in a dry season, and females that give birth a month after the peak of the wet season will likely have conceived during the dry season. Our results therefore suggest that some pregnancies are timed so that pups are born during the rainy season, when food is most available, whilst other pregnancies are carried when food is most available, leaving the resultant litters to be raised when food is scarcer. This is illustrated by Fig. 5, where birth rates peak around the height of the wet seasons (April/May and October), but there are also secondary peaks during the early dry seasons (in July and December).

The fact that gestation and pup care extends beyond the length of a single rainy season may explain why banded mongoose reproduction is not as seasonal as one might expect; births occur in all months of the year and are not confined to the wet season. It also suggests that females may be constrained in their reproduction by their gestation period. Such a trade-off in reproductive timing, where females can either maximise seasonal resource availability when gestating their offspring or when their offspring are growing after birth (but not both) may also lead to heretofore unrecognised condition-dependent decisions over when to reproduce. For instance, if the dominant females (who appear to control the timing of reproduction within a group (Cant *et al.* 2014)) are in relatively poor condition then the best option for them may be to conceive at during the rainy season when they can gain sufficient energy to carry the pregnancy. Whereas if dominant females are in better condition, they may be better giving birth when resources are more available for pup growth.

Previous trends in rainfall in western Uganda from 1983-2017 show that the first wet season (March-May) has been extended by 27 days and has experienced a 71% increase in rainfall (Diem *et al.* 2019b); if this trend continues, the timeframe under which banded mongooses can reproduce under optimum conditions may also increase. Depending on how much the duration of the wet seasons extends by in the future this could potentially reduce constraints on females, allowing them to time reproduction so that they are able to experience high resource availability for a greater proportion of each breeding attempt.

We found that high seasonal temperatures had a positive effect on pregnancy rates and number of foetuses carried by the mother. Females that conceive shortly after the increase in temperature early in the year (February) give birth at the peak of rainfall (April/May), while those that conceive after the increase in temperature later on in the year (August/September) give birth at the peak of the second rainy season (Oct/Nov). Changes in temperature are a well know cue for reproduction in a number of temperate bird species (Visser *et al.* 2009; Schaper *et al.* 2012; Martin *et al.* 2020) but have rarely been shown to be a cue for equatorial mammals (but see Heideman and Bronson (1994)). While we cannot exclude the possibility that higher temperatures are simply correlated with other variables that related to fecundity, it is possible that this represents a rare example of an equatorial mammal using small changes in temperature to predict future food availability for reproduction. The types of cues used by seasonally breeding equatorial mammals that cannot rely on changes in photoperiod to predict increases in rainfall and food availability has received very little attention previously.

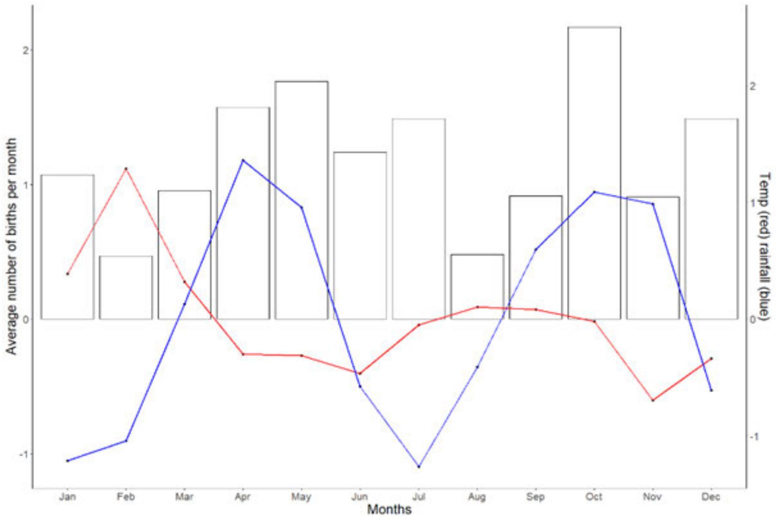


Figure 5. The mean number of births per group per month with seasonal rainfall (blue line) and maximum seasonal temperature (red line) overlayed.

2.4.2 Long- and short-term environmental changes effect parturition rates and number of foetuses produced

We predicted that, due to impacting food supply, long-term periods of low rainfall would lead to declines in birth (but not necessarily pregnancy) rates, and foetus numbers, whereby unseasonably low rainfall in the short-term may lead to increased likelihood of foetuses being aborted. Consistent with this, our results show that increasing long-term trends in rainfall positively affected parturition rates. However, unexpectedly, the impact of changing rainfall on parturition rates was dependent on temperature. Females were more likely to give birth as conditions got warmer and wetter and were least likely to give birth during cooler, dry conditions. Current evidence suggests that the region of Uganda that our study population is found in is going to experience wetter (Diem *et al.* 2019a, b) and warmer (Babel & Turyatunga 2015; Asefi-Najafabady *et al.* 2018) conditions over time. Based on our maximal model, if the average level of rainfall (1.98mm) becomes 0.5mm higher, this may lead to a 27.7% increase (0.256 to 0.327) in parturition rates. This positive effect may be exacerbated by the fact that high rainfall is also found to have a positive effect on other life stages including pup survival to emergence (chapter 2) and independence (Nichols et al. 2012). Similarly, if average temperatures (29°C) rise by 1°C, this could result in a 20% increase (0.256 to 0.306) in parturition rates, and if temperatures rise by 2°C, parturition rates could rise by 39.5% (0.256 to 0.357). Increases in long-term temperatures and rainfall outside of the range experienced in our data (26.5°C – 31.4°C and 0.637-3.00mm) however, may have differing impacts that are harder to predict. Furthermore, the positive associations of high temperatures with parturition rates may be counteracted by its negative effects on pup survival to emergence, pup survival to independence and helping behaviour (Chapter 3). We are also unaware how high temperatures might impact adult survival. Finally, the mechanism behind the link between high temperature and parturition rates is still unknown, and without first understanding this it is difficult to reliably predict future population trends.

Counter to our predictions, long-term trends in rainfall did not impact on the number of foetuses carried, suggesting that resource availability does not affect fecundity over and above its effect on parturition rates. However, long-term trends in temperature interacted with group size to predict the number of foetuses carried by pregnant females. Whilst medium and large groups appeared unaffected across different temperatures, perhaps indicating a buffering effect of cooperative groups to harsh conditions (Covas *et al.* 2008; Groenewoud & Clutton-Brock 2021), there was a sharp decline in the number of foetuses produced by females from small groups when temperatures increased. Based on our model predictions, if average long-term temperatures rise by 1°C, the number of foetuses carried by females in small groups will be reduced by 55.3%. So, if temperatures continue to increase across Uganda, as predicted by (Babel & Turyatunga 2015), females from small groups may produce increasingly smaller litters. This could also result in an Allee effect whereby in smaller groups there are fewer births leading to a lower recruitment, reducing the group size further (Stephens *et al.* 1999).

We also predicted that high short-term temperatures (which may represent heat waves) would cause heat stress in females, which may reduce fecundity. However, we found little evidence that pregnancy rates, birth rates or foetus counts were lower when short-term temperatures were high. The one exception was that the proportion, but not number, of females giving birth was lower under short-term high temperatures. It has previously been shown that when female banded mongooses suffer from elevated glucocorticoid concentrations (which is thought to be stress induced) during pregnancy, they have a lower reproductive success (Sanderson *et al.* 2015a). Hence, unexpectedly high temperatures could potentially cause stress which reduces reproductive success. Sudden heatwaves, which are also predicted to occur more frequently under climate change models (Meehl & Tebaldi 2004), may therefore counteract the benefits of high long-term and seasonal temperatures discussed above.

2.5 Conclusion

Our study finds that although banded mongooses give birth year-round, they are able to time reproduction to match peak environmental conditions by carrying pregnancies either: 1) during the dry season when food is more limited and giving birth during the wet season when food is abundant or 2) during the wet season and giving birth during the dry season. If, however, rainfall continues to increase over time and wet seasons become longer, females may be able to conceive and give birth over the course of a single wet season and reproduction may become concentrated towards specific times of the year. Seasonality is therefore important for reproduction in these equatorial mammals, though its impact may change over time. We also find potential evidence of females using high seasonal temperatures as a cue to enter oestrus in order to give birth when food availability is high, this may provide some of the first insights into the reproductive cues used by equatorial species. Finally, we are able to shed some light on the effect of long-term climatic trends on reproduction in an equatorial mammal. Our study shows that as conditions in Uganda continue to get hotter and wetter, parturition rates might increase over time, however it is difficult to predict how this will affect future recruitment since high temperatures also negatively affect survival.

2.7 Supplementary material

2.7.1 Methods

Modelling the proportion of females pregnant and giving birth in each group

We modelled the proportion of females pregnant or giving birth in each group using the cbind function in R. We based the proportion on the number of females over 9 months old within the group, since this is the age at which females can start to reproduce (Gilchrist *et al.* 2004).

2.7.2 Results

Pregnancy rates

Table S1: Model comparison table showing the competing models from the number of pregnancies analysis. This includes the name of the model, the number of parameters (K), logLik (log-likelihood), AIC, deltaAICc (the difference between the best model and every other model), Weight (model probabilities) and Evidence ratio (the amount of evidence for the best model relative to each model i.e. a score of 2 means that there is 2 times less evidence supporting it than the best model). Models with S in their name are from the first stage of the modelling process where only seasonal variables are modelled. Models with R in their name refers to the second stage where short-term changes variation in environmental variables are added. Models with T in their name refers to the final stage where long-term changes in environmental variables are added. The null model contained only group size and group size squared. The final model selected is in bold.

Model	K	logLik	AICc	deltaAICc	Weight	Evidence ratio
S3	**7**	**-2065.65**	**4145.30**	**0.00**	**0.32**	**1**
T2	8	-2065.61	4147.22	1.92	0.12	2.61
R1	8	-2065.61	4147.23	1.92	0.12	2.62
T1	8	-2065.63	4147.25	1.95	0.12	2.65
S4	8	-2065.63	4147.25	1.95	0.12	2.65
R3	9	-2065.50	4149.01	3.70	0.05	6.37
T3	9	-2065.61	4149.21	3.91	0.05	7.07
R4	10	-2064.70	4149.40	4.10	0.04	7.75
R2	10	-2065.28	4150.56	5.26	0.02	13.87
T4	10	-2065.52	4151.040	5.74	0.02	17.61
S2	6	-2072.72	4157.45	12.14	0	433.59
S1	6	-2076.04	4164.08	18.77	0	11934.70
Null	5	-2077.06	4164.12	18.81	0	12178.63

Table S2: Model comparison table showing the competing models from the proportion of pregnancies analysis. This includes the name of the model, the number of parameters (K), logLik (log-likelihood), AIC, deltaAICc (the difference between the best model and every other model), Weight (model probabilities) and Evidence ratio (the amount of evidence for the best model relative to each model i.e. a score of 2 means that there is 2 times less evidence supporting it than the best model). Models with S in their name are from the first stage of the modelling process where only seasonal variables are modelled. Models with R in their name refers to the second stage where short-term changes variation in environmental variables are added. Models with T in their name refers to the final stage where long-term changes in environmental variables are added. The null model contained only group size and group size squared. The final model selected is in bold.

Model	**K**	**logLik**	**AICc**	**deltaAICc**	**Weight**	**Evidence ratio**
S3	**6**	**-1763.71**	**3539.41**	**0.00**	**0.27**	**1**
T1	7	-1763.51	3541.01	1.60	0.12	2.23
T2	7	-1763.63	3541.26	1.85	0.11	2.52
R2	7	-1763.67	3541.35	1.94	0.10	2.64
S4	7	-1763.68	3541.35	1.94	0.10	2.64
R1	7	-1763.70	3541.41	1.99	0.10	2.71
S2	5	-1766.43	3542.85	3.44	0.05	5.59
T3	8	-1763.51	3543.01	3.60	0.04	6.05
R3	8	-1763.67	3543.35	3.94	0.04	7.17
T4	9	-1763.12	3544.24	4.83	0.02	11.19
Null	4	-1768.31	3544.62	5.21	0.02	13.55
R4	9	-1763.35	3544.70	5.29	0.02	14.08
S1	5	-1767.71	3545.42	6.01	0.01	20.18

Table S3. The proportion of pregnant females (out of the total number of females over 9 months) per group per month as a function of group size and environmental conditions in the previous month.

Fixed effects	Estimate	SE	z-value	p-value
(intercept)	-7.460	0.308	-24.3	
Group size	-0.782	0.150	-5.22	1.82×10^{-7}
Group size^2	0.043	0.120	0.357	0.721
Maximum seasonal temperature (in the previous month)	0.470	0.167	2.81	0.00490
Seasonal rainfall (in the previous month)	0.383	0.165	2.32	0.0202

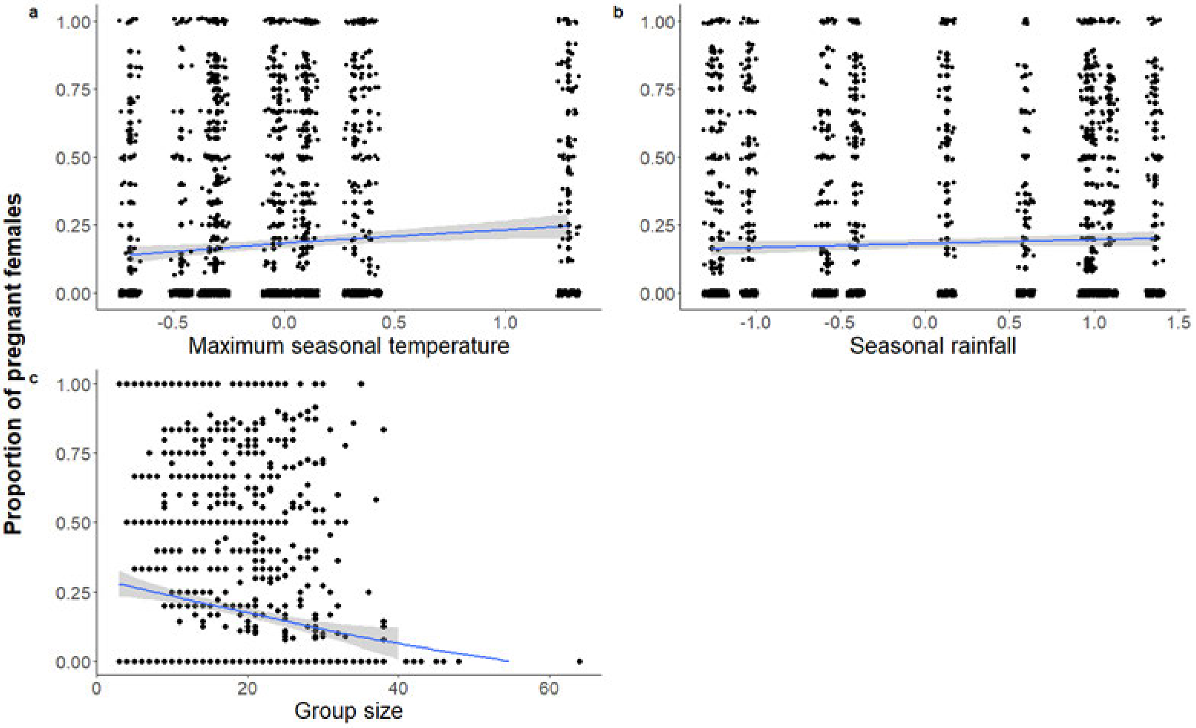


Figure S1. The proportion of pregnant females per group per month as a function of a) maximum seasonal temperatures, b) seasonal rainfall and c) group size.

Parturition rates

Table S4: Model comparison table showing the competing models from the number of births analysis. This includes the name of the model, the number of parameters (K), logLik (log-likelihood), AIC, deltaAICc (the difference between the best model and every other model), Weight (model probabilities) and Evidence ratio (the amount of evidence for the best model relative to each model i.e.. a score of 2 means that there is 2 times less evidence supporting it than the best model). Models with S in their name are from the first stage of the modelling process where only seasonal variables are modelled. Models with R in their name refers to the second stage where short-term changes variation in environmental variables are added. Finally, models with T in their name refers to the final stage where long-term changes in environmental variables are added. The null model contained only group size and group size squared. The final model selected is in bold.

Model	**K**	**logLik**	**AICc**	**deltaAICc**	**Weight**	**Evidence ratio**
T4	**9**	**-2605.36**	**5228.72**	**0.00**	**0.37**	**1**
T1	7	-2608.51	5231.02	2.30	0.12	3.16
T3	8	-2607.74	5231.48	2.76	0.09	3.97
R1	7	-2608.83	5231.65	2.93	0.08	4.33
R2	7	-2608.97	5231.94	3.22	0.07	5.01
S1	6	-2610.01	5232.02	3.29	0.07	5.19
S4	8	-2608.09	5232.17	3.45	0.07	5.62
R3	8	-2608.27	5232.55	3.83	0.05	6.77
R4	9	-2607.93	5233.85	5.13	0.03	13.00
T2	7	-2609.99	5233.99	5.27	0.03	13.91
S3	7	-2610.00	5234.01	5.29	0.03	14.05
S2	6	-2626.14	5264.27	35.55	0.00	52451470.00
Null	5	-2629.80	5239.80	40.87	0.00	750236600.00

Table S5: Model comparison table showing the competing models from the proportion of births analysis. This includes the name of the model, the number of parameters (K), logLik (log-likelihood), AIC, deltaAICc (the difference between the best model and every other model), Weight (model probabilities) and Evidence ratio (the amount of evidence for the best model relative to each model i.e.. a score of 2 means that there is 2 times less evidence supporting it than the best model). Models with S in their name are from the first stage of the modelling process where only seasonal variables are modelled. Models with R in their name refers to the second stage where short-term changes variation in environmental variables are added. Finally, models with T in their name refers to the final stage where long-term changes in environmental variables are added. The null model contained only group size and group size squared. The final model selected is in bold.

Model	**K**	**logLik**	**AICc**	**deltaAICc**	**Weight**	**Evidence.ratio**
R3	5	-2401.66	4813.32	0.00	0.19	1
R2	**4**	**-2402.91**	**4813.83**	**0.51**	**0.15**	**1.29**
R4	6	-2400.98	4813.97	0.65	0.14	1.38
R1	4	-2403.04	4814.09	0.77	0.13	1.47
T4	7	-2400.45	4814.90	1.58	0.09	2.20
T1	5	-2402.54	4815.07	1.75	0.08	2.40
T2	5	-2402.86	4815.71	2.40	0.06	3.32
S4	5	-2402.89	4815.79	2.47	0.06	3.44
T3	6	-2402.04	4816.08	2.76	0.05	3.97
S1	3	-2405.32	4816.63	3.31	0.04	5.24
S3	4	-2405.30	4818.61	5.29	0.01	14.10
S2	3	-2422.22	4850.44	37.12	0.00	114842400.00
Null model	4	-2426.34	4860.68	47.36	0.00	19243500000.00

Table S6. The proportion of female giving birth (out of the total number of females over 9 months) per group per month as a function of group size and environmental conditions in the previous.

Fixed effects	**Estimate**	**SE**	**z-value**	**P-value**
(intercept)	-4.28	0.242	-17.7	
Seasonal rainfall (in the previous month)	0.755	0.110	6.88	$6.09\mathrm{x}10^{-12}$
Short-term temperature (in the previous month)	-0.239	0.109	-2.20	0.0276

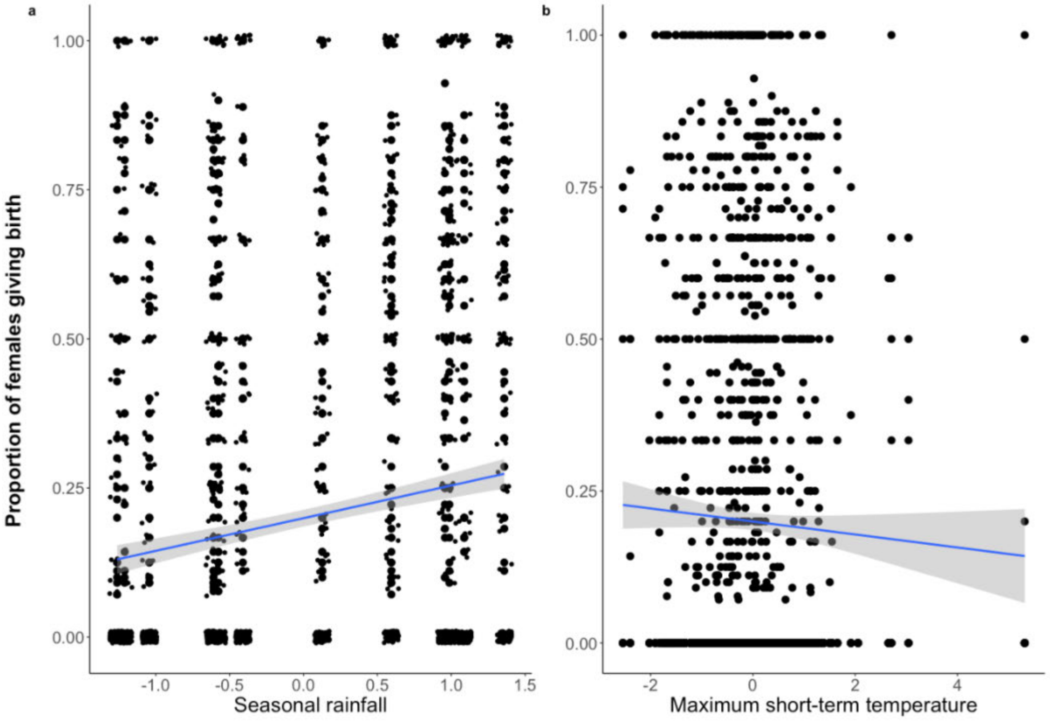


Figure S2. The proportion of females giving birth per group per month as a function of a) seasonal rainfall in the previous month and b) short-term temperature in the previous month.

3 High temperatures reduce offspring survival directly and indirectly (through reducing altruism) in cooperatively breeding banded mongooses

3.1 Abstract

Cooperative breeding has been proposed to buffer social groups against variable environmental conditions as helpers provide offspring care which may maintain survival during harsh conditions. However, the evidence is mixed, and previous studies have largely used group size as a proxy of helping effort, rather than assessing the latter directly. Using 20 years of data on banded mongooses (*Mungos mungo*), we found that hot, dry conditions reduced pup survival both directly and indirectly via reducing helping behaviour. Larger groups provided more help to young pups, leading to higher survival to 30 days. However, older pups from large groups received less help and had poorer survival to 90 days, and we found no evidence that larger groups outperformed smaller groups under poor conditions. Together, our results suggest that cooperative breeding does not buffer against harsh environmental variation, such as that caused by anthropogenic-driven climate change.

3.2 Introduction

Human-induced climate change has been found to have wide-ranging impacts on animal populations, causing population declines (Oppenheimer *et al.* 2015; WWF 2016), altering morphology and growth (Ozgul *et al.* 2009; Lackey & Whiteman 2022), and shifting distributions and phenology (Parmesan & Yohe 2003; Root *et al.* 2003; Cohen *et al.* 2018). Such effects have generated heightened interest in understanding the ways in which animals respond to changes in climate-related variables such as temperature and rainfall. While some changes are occurring over long time-periods, such as globally increasing temperatures and changes in the timing of seasons, others occur in the short-term, for example droughts, wildfires, and other extreme weather events (Mirza 2003; Badeck *et al.* 2004). Even brief fluctuations in environmental conditions can have potentially devastating impacts on animal populations, for example heatwaves and droughts can lead to declines in body condition (Gardner *et al.* 2016), increased risks of hyperthermia (McKechnie & Wolf 2010) and higher mortality rates (McKechnie *et al.* 2012; Bondarenco *et al.* 2014). It is therefore important to identify mechanisms that may lead to increased resilience of animal populations to long- and short-term fluctuations.

Many animals use behavioural means to cope with environmental change (Buchholz *et al.* 2019). For example, some species change their foraging strategy to stay hydrated during seasonal droughts (Sato *et al.* 2014), while others may rest in the shade or in water when temperatures increase (Jackson *et al.* 2009; Sawaya *et al.* 2017). Cooperative behaviour also has the potential to buffer against poor environmental conditions (Jetz and Rubenstein 2011; Russell et al. 2016). Cooperative breeding, whereby subordinate 'helpers' assist in raising the offspring of dominant breeders (Solomon & French 1997; Koenig & Dickinson 2016), spreads the cost of reproduction over multiple individuals, and thus may allow breeders to successfully reproduce even under poor environmental conditions (Sarhan & Kokko 2007; Covas *et al.* 2008). Supporting this hypothesis, cooperative breeding is positively correlated with harsh and unpredictable environments on a global scale across birds (Cornwallis *et al.* 2017) and mammals (Lukas & Clutton-Brock 2017). At the species-level, the presence of helpers has been shown to improve offspring provisioning rates to a greater extent under poor conditions in azure-winged magpies (*Cyanopica cyanus*) (Canário *et al.* 2004), and larger social groups have been shown to mitigate the negative effects of low rainfall on birth rates and pup survival in meerkats (*Suricata suricatta*) (Groenewoud & Clutton-Brock 2021), potentially because they are better able to provide pup care and to defend larger, high quality territories (Krause *et al.* 2002; Dyble *et al.* 2019).

However, the buffering effect of cooperative breeding is not universal (e.g. Koenig *et al.* 2011; (Bourne *et al.* 2020b; D'Amelio *et al.* 2022), because larger groups also impose more intense local resource competition, and this should become even more acute under poor environmental conditions (Pride 2005). The potential of cooperation to buffer groups from the effects of poor environmental conditions is therefore likely to depend on how individuals change their investment in cooperation when conditions get tough. Because cooperative behaviours are often costly (e.g. reducing helper weight) they often decline under poor environmental conditions (Clutton-Brock *et al.* 1998; Heinsohn 2004; Wiley & Ridley 2016). For example, meerkat helpers with poor body condition are more likely to abandon a litter (Russell *et al.* 2003b) and non-breeding banded mongooses (*Mungos mungo*) reduce their input to pup care when rainfall, an indicator of food availability, is low (Nichols *et al.* 2012a). Nevertheless, helping behaviour is generally assumed to increase with group size in empirical studies of buffering (e.g. Bourne *et al.* 2020a; Groenewoud & Clutton-Brock 2021), and the use of group size as a proxy of helping behaviour may complicate interpretations of a buffering effect of cooperation.

To further our understanding of the potential for cooperation to buffer group members against environmental variation, we need to disentangle the impact of the size of the social group from the effect of the behaviour of group members. Furthermore, we need to assess the contribution of direct impacts of environmental conditions on survival alongside the indirect impacts resulting from changes in helping behaviour. Our banded mongoose study population in Uganda provides an excellent opportunity to address these issues as we have gathered 20 years of detailed data on group composition, helping behaviour and fitness data (pup survival) on over 3000 individuals, along with environmental data documenting variation in temperature and rainfall. Here, we first evaluate the degree to which short-term, seasonal and long-term variation in rainfall and temperature have direct effects on survival or whether these effects are mediated by their impact on helping behaviour. Due to the importance of helping behaviour in determining pup survival (Hodge 2005), we predict that environmental variation will largely impact pup survival through changing the behaviour of care-givers. Second, we investigate whether larger social groups are buffered against the negative impacts of poor environmental conditions. If buffering occurs, we expect to find a positive relationship between group size and help provided to pups, leading to higher pup survival in large groups. Furthermore, we would expect to see interactions between group size and environmental variables, resulting in weaker impacts of poor environmental conditions in larger groups. If buffering does not occur, we expect to see direct impacts of poor conditions on survival that are unaffected by group size and helping behaviour.

3.3 Methodology

3.3.1 Study system and data collection

Our study uses behavioural, life history and environmental data collected from a population of wild banded mongooses in Mweya, Queen Elizabeth National Park, Uganda (0° 12’S, 27° 54’E) collected between June 2000 and July 2020. Our study site is located in a scrub-savannah habitat and can be characterised by relatively constant temperatures (as is expected from an equatorial region) and two rainy seasons per year. Our study population is habituated to observation at <10m (usually <5m) and social groups are visited every 1-3 days to collect behavioural data and determine group composition and individual survival (see Jordan et al. (2010) for further details). At any one time, the population is made up of approximately 250 individuals, split up into 10-12 groups, each of which typically contains between 10-30 adults (Cant *et al.* 2016). For our study, we defined group size as the number of individuals over 6 months old present in the group. We set this age limit since individuals under this age do not contribute to pup care, which is the focus of our study (Cant 2003; Gilchrist *et al.* 2004).

To quantify environmental variation, we used rainfall (mm) and maximum temperature (°C) data collected daily from Mweya meteorological station at the centre of our study site. High levels of rainfall have been shown to cause changes in vegetation and an increase in invertebrate abundance (Cant *et al.* 2013; Marshall *et al.* 2017). Since banded mongooses have a primarily insectivorous diet, periods of high rainfall have positive impacts on banded mongooses, leading increased helping effort (Nichols *et al.* 2012a) and heavier pups with higher survival chances (Nichols *et al.* 2012b). In contrast to rainfall, the effect of temperature has not been studied in banded mongooses. Variation in maximum daily temperature is small at our study site (monthly mean maximum daily temperature ± standard deviation [SD] = 29.5 ± 1.5 °C; Marshall et al. 2016). However, species that have evolved to live at constant temperatures may have very low thermal tolerances (Tewksbury *et al.* 2008), so even small changes in temperature could have physiological implications such as heat stress. We therefore decided to investigate the effect of both temperature and rainfall on survival and helping behaviour. Unlike previous studies, our study combines both the direct and indirect effects of environmental variables on survival under one model framework, and investigates both short and long-term environmental changes.

Each social group contains a core of dominant breeders (usually between 1-3 males and 3-7 females) which reproduce 3-4 times a year, although subordinates breed alongside them when conditions allow for it (Cant 2000; Bell 2010; Nichols *et al.* 2012b). Within groups, females reproduce synchronously, giving birth together (usually on the same day) and the pups are raised as a communal litter in an underground den. Pups receive two main forms of help from adult group-members; babysitting and escorting (Fig 1). After birth, pups are guarded from predators and rival groups by one or more adult 'babysitters' who remain at the den whilst the rest of the group forages. All adult group-members usually contribute to babysitting the pups for at least one foraging session, regardless of relatedness to the litter (Vitikainen *et al.* 2017). We classed an individual as babysitting if they were observed at the den with the pups during a foraging session, or if they were recorded as absent from the foraging group when the group was over 100m from the den (Hodge 2007). Litter survival was assessed based on whether any pups from the litter survived to 30 days, when they emerge from the den and start to accompany the group on foraging trips. Once emerged, most pups form a one-to-one relationship with an adult helper, known as an 'escort', which provides its pup with food and protection until the pups reach nutritional independence at ~90 days (Cant *et al.* 2013). Adults vary in the amount of escorting care they provide, and many adults do not escort a pup (Sheppard *et al.* 2018; Nichols *et al.* 2021). Following previous studies (Gilchrist *et al.* 2004; Sanderson *et al.* 2015b), an individual was considered to be escorting a pup when it was within 30cm of a particular pup for over half of an observation session, which lasted at least 20 minutes for both babysitting and escorting.

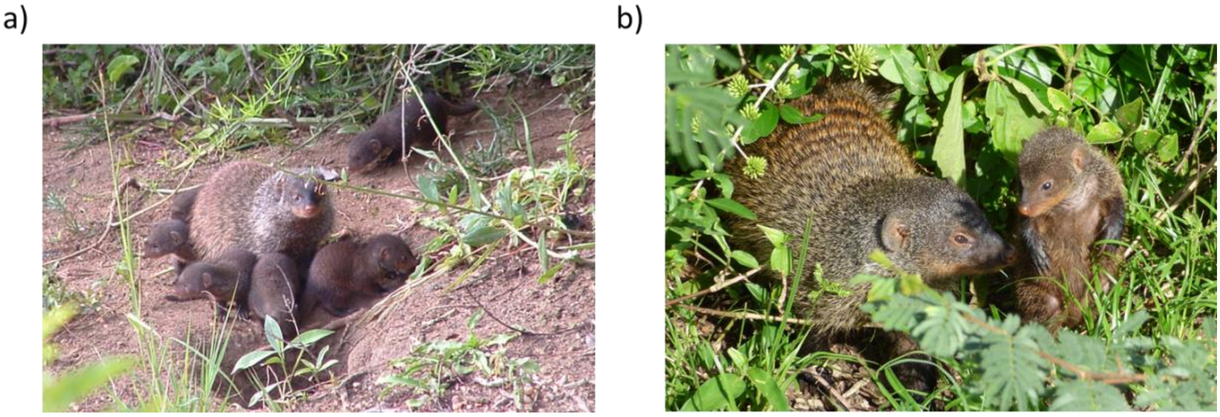


Figure 1. Helping behaviour in banded mongooses, with a) showing babysitting behaviour, whereby one or more adults remains at the den to guard very young pups (under 30 days old) from predators and rival groups while the rest of the group forages and b) showing escorting behaviour, where adults form 1:1 caring relationships with pups old enough to accompany the group on foraging trips (aged 30-90 days).

3.3.2 Statistical analyses

Decomposition of environmental variables

Seasonal variation in the environment can potentially confound shorter or longer-term variation in environmental variables (Groenewoud & Clutton-Brock 2021). Therefore, in this study we aimed to differentiate between short-term environmental fluctuation, seasonal variation and long-term trends. To do this, we decomposed a time series of our temperature and rainfall data into three main components: (1) seasonal variation, representing consistent intra-annual change (2) long-term trends in environmental changes over the 20-year duration of the study and (3) short-term environmental fluctuations, representing residual environmental variation after seasonal cycles and long-term trends are removed (Fig S1). Over the 20-year period of our study, for logistical reasons it was not always possible to collect daily environmental data (e.g. due to staff sickness or time constraints), resulting in a small proportion of missing values: 524 days (6.75%) for maximum temperature and 421 days (5.42%) for rainfall. Before decomposing our data, we filled in the missing values with estimated values using the imputeTS package (Moritz & Bartz-Beielstein 2017) in R version 4.2.1 (R Core Team 2022). Following this, we calculated monthly averages and subsequently formatted our data as a time series, which was then decomposed into seasonal variation and short-term environmental fluctuations in R version 4.2.1. (R Core Team 2022). The 'decompose' function estimated long-term trends using moving averages, seasonal cycles, and residual (short-term) variation remaining after accounting for seasonal and trend components. These environmental variables were used as fixed effects in our subsequent statistical models.

Statistical model construction

We used generalized linear mixed effects models (GLMMs) in R version 4.2.1. (R Core Team 2022) to investigate the effects of the probability of a litter being babysat (babysitting effort), the probability of a pup being escorted (escorting effort), environmental variables (rainfall and temperature), group size, and interactions between environmental variables and group size on 1) litter survival to emergence at 30 days (n=449 litters) and 2) pup survival from emergence to nutritional independence at 90 days (n=740 pups). Using the same datasets, we also tested the effects of environmental variables, group size and the interactions between the two on 3) babysitting effort and 4) escorting effort. All continuous explanatory variables in our models were scaled so that main effects could be interpreted in the presence of interactions (Schielzeth 2010). We used the 'BOBYQA' optimizer algorithm in all of our GLMMs to deal with convergence issues (Bates *et al.* 2015). As multiple observations were taken from the same social groups, we fitted group identity as a random effect in our models, except where an observation level random effect was used to address over-dispersion. Standard model checks were employed following Crawley (2015). See the supplementary information for further information on model construction and selection.

To disentangle the direct and indirect effects (via influencing helping behaviour) of environmental conditions and group size on survival, we created two piecewise structural equation models (SEM) using the R package PiecewiseSEM (Lefcheck 2016). First, to investigate these relationships during the babysitting period, when pups are reared in communal litters and babysat in the den, we combined all of the significant effects from the best litter survival to emergence and babysitting effort GLMMs into an SEM (Table 1). Similarly, to investigate these relationships at the escorting stage, when pups are cared for on a one-to-one basis, we combined the best pup survival to independence and escorting effort GLMMs into a SEM. Before constructing an SEM from the GLMMs, any non-significant variables were removed. Once the SEM was created, variables with no direct path between them were assumed to be independent; these are known as 'independence claims'. We used p-values from Shipley's test for directional separation to calculate a global goodness-of-fit measure, which indicated whether all the important relationships among variables in our dataset were captured by the SEM (Lefcheck 2016).

3.4 Results

3.4.1 Impact of environmental conditions and group size on babysitting and litter survival

Our SEM (Fig 2) found that only two variables directly impacted on litter survival to 30 days; high seasonal temperatures reduced litter survival (estimate = -0.286 ± 0.109, z-statistic = -2.61, p=0.00896) whilst high levels of babysitting effort increased litter survival (estimate = 0.590 ± 0.109, z-statistic = 5.40, $p=6.57x10^{-8}$) (Fig S2, Table 1). Litters that were babysat every day they were observed had an 87% chance of surviving to 30 days, whereas litters never observed with a babysitter had only a 30% chance of survival. Three further variables had indirect positive impacts on pup survival via increasing babysitting behaviour; increases in group size (estimate =0.312 ± 0.0749, z-statistic = 4.17, $p=3.04x10^{-5}$), high seasonal rainfall (estimate = 0.245 ± 0.0731, z-statistic = 3.35, $p=8.00x10^{-4}$) and long-term increases in rainfall (estimate = 0.252 ± 0.0739, z-statistic = 3.41, $p=6.51x10^{-4}$) (Fig S3, Table 1).

Independence claims from the SEM were all nonsignificant, suggesting that the meaningful relationships between variables in our dataset were described by the paths specified in our piecewise SEM (Table S6). The p-values from these independence claims were used to calculate a global goodness-of-fit measure, which indicated that the important relationships among variables in our dataset were captured by the SEM (Fisher's C = 7.103, d.f. = 8, p-value = 0.526) (Lefcheck 2016). The models incorporated into this SEM explained a relatively small amount of the variance in our response terms (13% for litter survival to 30 days and 15% for babysitting effort) (Table S5). This was unsurprising since there are a multitude of social, behavioural, physiological, and environmental factors that can affect both survival and helping behaviour, and we were not able to measure them all in our long-term study.

Table 1. Fixed effects and their significance for the two models (litter survival and babysitting effort) that made up our piecewise structural equation model.

Response	**Fixed effects**	**Estimate**	**SE**	**z-value**	**P-value**
Litter survival to 30 days (n=449)	(Intercept)	1.17	0.117	10.0	
	Maximum seasonal temperature	-0.286	0.109	-2.61	0.00896
	Proportion of time babysitting	0.590	0.109	5.40	6.57x10^{-8}
Babysitting effort	(intercept)	1.79	0.0771	23.29	
	Seasonal rainfall	0.245	0.0731	3.35	8.00x10^{-4}
	Group size	0.312	0.0749	4.17	3.04x10^{-5}
	Long-term rainfall	0.252	0.0739	3.41	6.51x10^{-4}

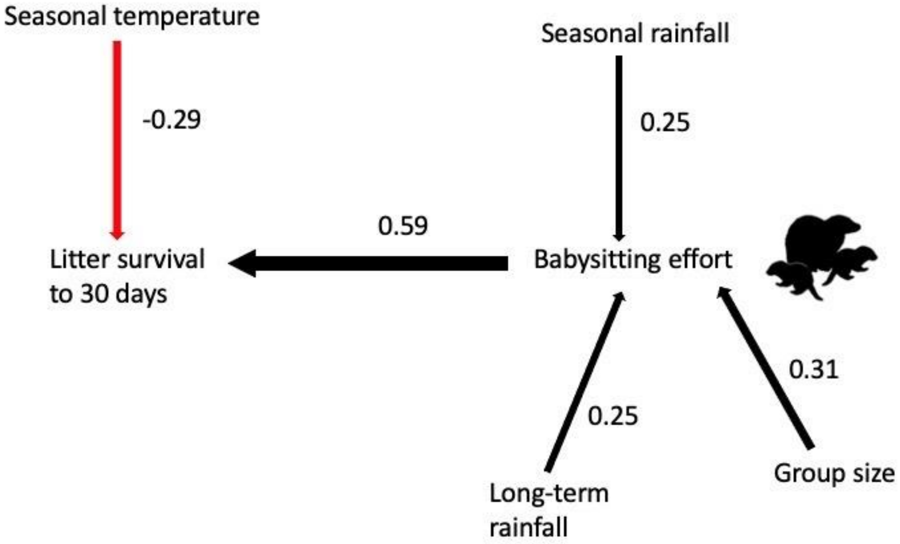


Figure 2. Piecewise structural equation model incorporating both the best litter survival and babysitting effort model. Arrows represent the relationships between variables with their width directly relating to the size of the corresponding coefficient. Black arrows represent positive relationships whereas red arrows represent negative relationships.

3.4.2 Impact of environmental conditions and group size on escorting and pup survival

Our second SEM (Fig 3, Table 2) uncovered a complex network of variables that interact to determine pup survival. Helping behaviour, group size and five environmental variables had direct impacts on survival, and four of these environmental variables interacted with group size to influence survival. Survival was also impacted indirectly through influencing helping behaviour; group size and three environmental variables impacted on escorting effort, with three of the environmental variables interacting with group size to determine escorting effort.

The probability that a pup survived to independence at 90 days increased with the proportion of time it was escorted (estimate = 0.715 ± 0.101, z-statistic = 7.10, $p=1.29\times10^{-12}$) (Fig S4). Pups observed being escorted 100% of the time during the escorting period had an 87% chance of surviving to 90 days whereas pups that were never observed with an escort had only a 47% chance of survival. However, pups were slightly less likely to be escorted in larger groups (estimate = -0.351 ±0.0508, z-statistic = -6.98, p-value=3.02×10^{-12}), so larger groups are unlikely to outperform smaller groups in challenging conditions through offering more help to pups. After controlling for the impact of group size on helping behaviour, we found no evidence that larger groups do better when conditions are poor; pup survival in large groups was similar to or worse than medium and small groups under harsher environmental conditions (high temperatures and low rainfall) (Fig 4). Surprisingly, smaller groups had the highest pup survival when seasonal and long-term temperatures were high (Fig 4c and d), while medium sized groups had the highest pup survival when seasonal and short-term rainfall was low (Fig 4a and b).

Similar to the babysitting SEM, we found direct negative impacts of high temperatures on pup survival; pups were less likely to survive when short-term temperatures were high (estimate = -0.213 ± 0.104, z-statistic = -2.04, p=0.0414) (Fig S4b). We also found a significant interaction between seasonal rainfall and maximum seasonal temperature (estimate = 0.306 ± 0.125, z-statistic = 2.45, p = 0.0142) (Fig S4c); at high maximum seasonal temperatures, the probability of pups surviving to independence increased during seasons of high rainfall. On the other hand, at medium to low maximum seasonal temperatures, increases in seasonal rainfall reduced pup survival.

As with our babysitting SEM, independence claims were found to be nonsignificant. The global goodness-of-fit measure also indicated that the important relationships among variables in our dataset were captured by the SEM (Fisher’s C =5.884, d.f.=4, p=0.211) (Lefcheck 2016). The models incorporated into this SEM explained around a quarter of the variance in our response terms (24% for survival to independence and 26% for escorting effort) (Table S5).

Table 2. Fixed effects and their significance for the two models (pup survival to independence and escorting effort) that made up our piecewise structural equation model.

Response	Fixed effects	Estimate	SE	z-value	P-value
Pup survival to 90 days (n=740)	(Intercept)	1.275	0.246	5.19	
	Maximum seasonal temperature	-0.313	0.160	-1.96	0.0498
	Group size	-0.204	0.116	-1.75	0.0798
	Group size (sq)	-0.221	0.098	-2.27	0.0233
	Seasonal rainfall	-0.120	0.152	-0.789	0.430
	Short-term rainfall	-0.250	0.139	-1.80	0.0723
	Maximum short-term temperature	-0.213	0.104	-2.04	0.0414
	Maximum long-term temperature	-0.339	0.132	2.46	0.0104
	Escorting index	0.715	0.101	7.10	1.29x10^{-12}
	Maximum seasonal temperature: Group size	-0.264	0.129	-2.04	0.0416
	Maximum seasonal temperature: Group size (sq)	0.308	0.125	2.46	0.0139
	Group size: Seasonal rain	-0.0522	0.970	-0.539	0.590
	Group size (sq): Seasonal rain	0.348	0.100	3.48	5.09x10^{-4}

	Maximum seasonal temperature: Seasonal rain	0.306	0.125	2.45	0.0142
	Group size: Short-term rainfall	-0.301	0.118	-2.56	0.01034
	Group size (sq): Short-term rainfall	0.324	0.128	2.54	0.0111
	Group size: Maximum long-term temperature	-0.153	0.125	-1.23	0.220
	Group size (sq): Maximum long-term temperature	0.260	0.0953	2.73	0.00637
Escorting effort	(Intercept)	0.202	0.0646	3.12	
	Seasonal rain	0.0975	0.0680	1.44	0.151
	Group size	-0.351	0.0508	-6.98	3.02x10^{-12}
	Group size (sq)	0.0233	0.0452	0.516	0.606
	Maximum short-term temperature	-0.0265	0.0700	-0.378	0.706
	Maximum long-term temperatures	-0.1106	0.0510	-2.17	0.0301
	Seasonal rain: Group size	0.0338	0.0470	0.720	0.472
	Seasonal rain: Group size (sq)	-0.134	0.0426	-3.14	0.00167
	Group size: Maximum short-term temperature	-0.159	0.0619	-2.56	0.0103
	Group size (sq): Maximum short-term temperature	-0.157	0.0712	-2.21	0.0272

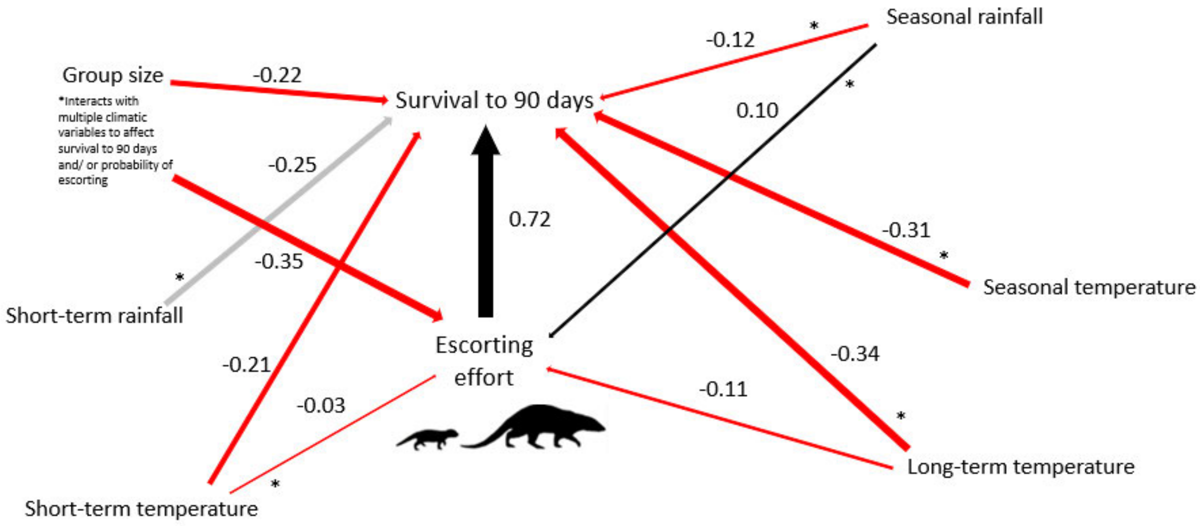


Figure 3. Path diagram representing the piecewise structural equation model which incorporates both the best pup survival to 90 days and escorting effort model. Arrows represent the main relationships between variables with their width directly relating to the size of the corresponding coefficient. Black arrows represent positive relationships whereas red arrows are used to represent negative relationships. An asterisk next to an arrow indicates that apart from the main relationship shown, the variable also interacts with group size to significantly affect escorting or survival to 90 days. A grey arrow was used where a variable significantly interacted with group size to affect a variable but did not have a significant main effect.

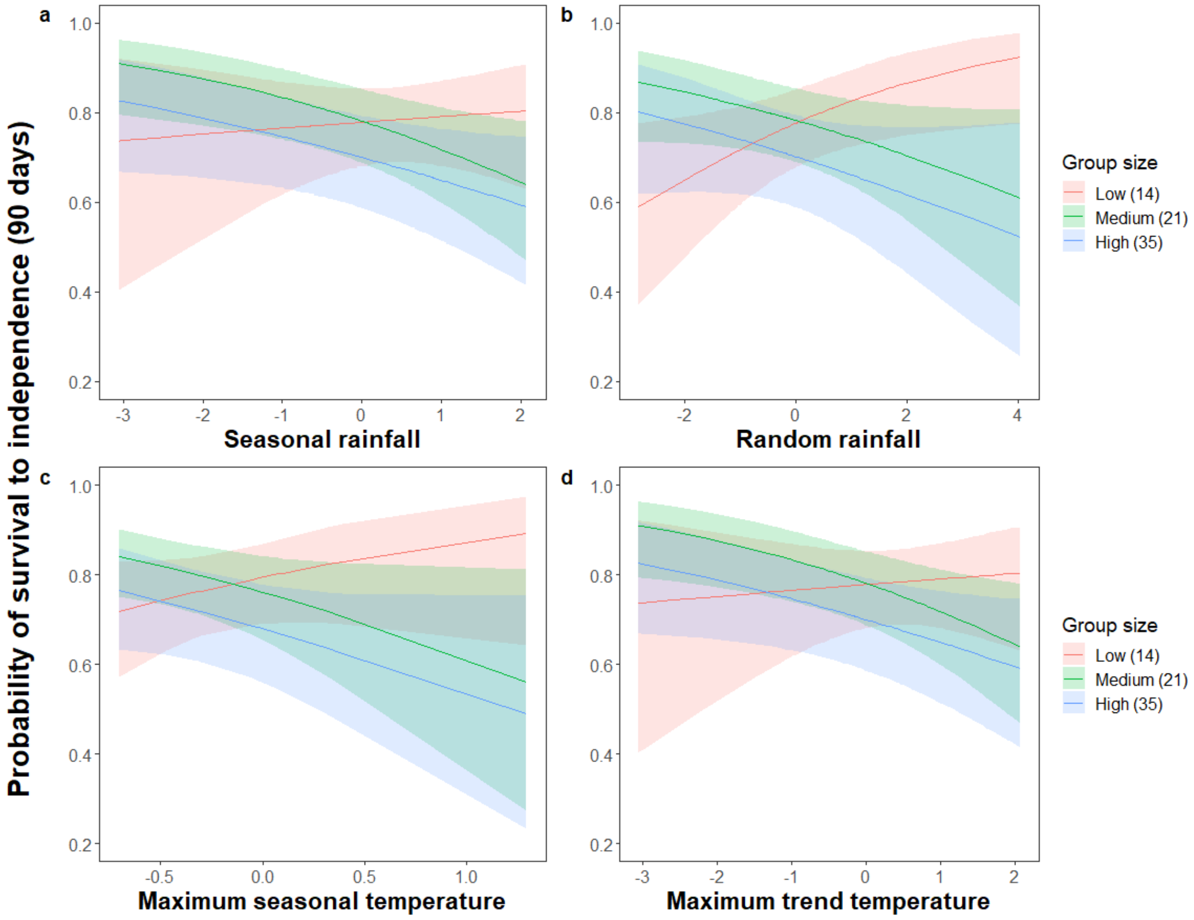


Figure 4. The probability of pups surviving to independence as a function of (a) seasonal fluctuations in rainfall, (b) short-term variation in rainfall, (c) seasonal temperature and (d) long-term temperature at different group sizes.

3.5 Discussion

Our study reveals that hot, dry conditions reduce offspring survival because of two causal pathways, first by directly reducing early life survival, and second, indirectly, by reducing the amount of alloparental investment they receive from adult helpers to offspring care. This highlights the importance of investigating causal pathways to determine how environmental change impacts populations. Most previous studies have solely focused on the direct effects (on either helping behaviour, group size or survival) with few studies attempting to investigate the flow of causality (but see Bourne, Cunningham, Spottiswoode, et al. 2020). We found very limited evidence that large groups buffered pups from adverse conditions. While larger groups provided more babysitting to pups, and therefore had higher litter survival to 30 days, larger groups provided less escorting care to pups, which in turn had lower pup survival between 30 and 90 days. Furthermore, although we found interactions between group size and environmental variables that impacted both escorting and pup survival between 30 and 90 days, they did not result in weaker impacts of poor environmental conditions in larger groups. Given the projected increases in temperatures of the region with anthropogenic climate change (Anyah & Qiu 2012; Babel & Turyatunga 2015), the impacts of temperature on helping behaviour and pup mortality are concerning.

3.5.1 Direct and indirect impacts of poor environmental conditions on pup survival

Our results show that environmental conditions had substantial indirect impacts on banded mongoose pup survival through changing contributions to helping behaviour. The main determinant of pup survival was the amount of care that pups received from helpers, which is reflective of the critical role that helpers play in cooperatively breeding species (Snowdon & Cronin 2007; Kingma *et al.* 2010). In banded mongooses, babysitters protect pups from predators and attacks from rival groups (Cant *et al.* 2013), while escorts feed, carry and protect pups, leading to higher rates of growth and survival (Gilchrist 2004; Hodge 2005; Vitikainen *et al.* 2019). We found that babysitting effort reduced when seasonal and long-term rainfall was low, while escorting effort decreased with reductions in seasonal rainfall and increases in temperature over both long and short periods. Dry conditions lead to declines in the abundance of the invertebrates that banded mongooses feed on (Cant *et al.* 2013; Marshall *et al.* 2017), in turn reducing contributions to care (Nichols *et al.* 2012a). Banded mongooses are also found to behaviourally thermoregulate by foraging less under hotter conditions temperatures (Chapter 5). Behavioural thermoregulation has been found in many species (Carroll *et al.* 2015b) and can include seeking cooler microsites and reducing activity levels (Váczi *et al.* 2006; Cunningham *et al.* 2015). The reductions in banded mongoose helping behaviour that occur in hot and dry conditions imply that sustained droughts and heat waves indirectly lead to lower pup survival through reducing contributions to care.

While some environmental variables impacted on helping behaviour, others directly influenced pup survival. High seasonal temperatures reduced pup survival, regardless of how often the litter was babysat, and at the escorting stage, all bar one of our environmental variables impacted directly on pup survival. Higher seasonal temperature reduced pup survival, without affecting escorting behaviour. Furthermore, high temperatures over short and long periods both directly reduced pup survival and also had a negative effect on escorting behaviour. The combination of direct and indirect effects of hot conditions may therefore lead to an amplified negative impact on pup survival.

High temperatures have also been shown to reduce offspring survival in other southern African species. For example, southern pied babbler nestlings have lower survival at high temperatures (Bourne *et al.* 2020a), likely because of a reduction in adult provisioning rates (Wiley & Ridley 2016). Similarly, in African wild dogs (*Lycaon pictus*), foraging time is shorter at high temperatures (Woodroffe *et al.* 2017), and it is proposed that adults struggling to meet food intake requirements may not prioritise babysitting, resulting in pups being more vulnerable to predation (Courchamp *et al.* 2002). High temperatures may be particularly problematic in the tropics because endothermic species living in equatorial regions often have a narrow climatic tolerance as they are adapted to relatively stable temperatures (West 2003; Carroll *et al.* 2015a). This may explain why small changes in temperature had significant effects on banded mongoose offspring survival, and implies that this population may be vulnerable to future population declines given that Uganda is expected to experience a 1-2°C warming by 2050 (Anyah & Qiu 2012).

3.5.2 Limited buffering effect of group size

We found minimal evidence for buffering occurring in banded mongooses; litters belonging to larger groups received more babysitting, which in turn increased their probability of survival. However, we found no evidence that larger groups compensated for poor conditions by boosting babysitting effort; none of the environmental variables interacted with group size to predict helping or survival, and high temperatures reduced litter survival regardless of group size. This suggests that, whilst being in a larger group is beneficial for very young pups, larger groups cannot always buffer their pups against poor environmental conditions.

Although larger groups boost litter survival at the babysitting stage, perhaps by protecting from intergroup infanticide and predation, we found no evidence that this effect extends to the escorting stage. In contrast, pups from larger groups were less likely to be escorted and less likely to survive to nutritional independence than pups from smaller groups. While group size interacted with multiple environmental variables to influence escorting effort and pup survival, we did not find evidence that larger banded mongoose groups do better in poor conditions. Differences in the impact of group size during the babysitting and escorting periods may be due to the differing cost-benefit ratio of these activities as group size increases. As the number of babysitters that stay behind to protect the litter does not increase significantly with group size (Cant 2003), adults in larger groups can reduce their individual input into babysitting whilst maintaining the level of care that pups receive. This sharing of responsibility to reduce per-capita investment is known as 'load lightening' (Woxvold & Magrath 2005; Meade *et al.* 2010) and is seen across multiple cooperatively breeding species including superb fairy-wrens (*Malurus cyaneus*) (Langmore *et al.* 2016), florida scrub-jays (*Aphelocoma coerulescens*) (Mumme *et al.* 2015), long-tailed tits (*Aegithalos caudatus*) (Hatchwell 1999) and meerkats (*Suricata suricatta*) (Clutton-Brock *et al.* 2004). In contrast, we may not see load lightening at the escorting stage as larger groups have larger communal litters, which require more escorts to care for them as escorting usually occurs on a 1:1 basis (Cant *et al.* 2013). This may negate the benefit of having more helpers, explaining why we found that escorting effort does not increase with group size; in fact, escorting effort was reduced in larger groups. Under poor conditions, potential helpers belonging to larger groups may face higher competition for food compared to smaller groups making them more likely to prioritise their own survival over offspring care.

Taken together, our results suggest that larger groups have a very limited ability to buffer their pups against harsh conditions. This is in contrast to the situation that has been proposed in some other cooperative species including sociable weavers (*Philetairus socius*) (Covas *et al.* 2008), superb starlings (*Lamprotornis superbus*) (Rubenstein 2011) and meerkats (*Suricata suricatta*) (Groenewoud & Clutton-Brock 2021). Unlike these studies however, which used group size as a proxy for helping effort, we studied the effects of helping effort and group size separately, which has allowed us to dismantle their impacts. It is likely that species-level differences in the potential of cooperative groups to buffer against environmental change are determined by the relationships between group size, helping behaviour and environmental conditions, with only some cooperative species benefiting from buffering under harsh environments. Understanding the determinants of this relationship will help us to understand the potential impacts of anthropogenic climate change on cooperative breeders.

3.7 Supplementary information

3.7.1 Method

Behavioural data collection

All banded mongoose groups were habituated to allow observation at <10m. For identification of individuals in the field, mongooses were either marked with a unique pattern of hair dye (L'Oreal UK) or a unique shave pattern in their fur. Some adults were given colour-coded plastic collars for identification. All individuals were trapped and anaesthetised every 3-6 months so that their shave patters, markings, and collars could be maintained (Cant 2000; Hodge 2007; Jordan *et al.* 2010). When individuals were first captured, they were visually inspected to determine sex and were given either a uniquely coded tattoo or (since 2001) a pit tag (TAG-P-122IJ, Wyre Micro Design Ltd., UK) so that they could be permanently identified. Radio collars weighing 27g (< 2% of body mass; Sirtrack Ltd., New Zealand) with a 20cm whip antenna were attached to 1 or 2 individuals per group allowing them to be tracked. Each group was visited every 1-3 days to collect behavioural and life history data. Females give birth overnight in an underground den and so births were identified by the absence of pregnant females the following morning along with a sudden change in the females body shape and mass loss (Gilchrist 2006b; Hodge *et al.* 2011).

Statistical analyses

Attempting to model all 6 potential interactions between environmental variables and group size plus the 6 potential interactions between group size squared (to account for non-linear effects) and environmental variables as well as main effects in one model led to a singular fit. To avoid fitting an overly complex model we took an information theoretical approach to model selection, comparing biologically plausible models with nulls using Akaike Information Criterion (AIC) and selecting the best fitting model (Johnson & Omland 2004; Arbuckle & Minter 2015; Matuschek *et al.* 2017). We used prior knowledge of banded mongoose biology to construct biologically realistic models in three stages. Comparing the maximal model to the best model from our selection table we also found that the maximal model had a much higher AIC value. Standard model checks were employed following Crawley (2015).

Stage 1: We started off by constructing models with seasonal environmental variables, which are likely to be important as banded mongoose breeding is to some extent seasonal, peaking during the rainy seasons. We started with a null model where the response variable was only modelled as a function of group size (and helping behaviour in the case of litter and pup survival models). This null model was used as a base to create four other models that incorporated seasonal fluctuations. The first model (S1) included seasonal rain (plus interactions between group size and seasonal rain); the second model (S2) included seasonal temperature (plus interactions between group size and seasonal temperature); the third model (S3) included seasonal rain and seasonal temperature (along with the interactions between the seasonal variables and group size); the fourth model (S4) was the same as the third model with the addition of an interaction term between seasonal rain and seasonal temperature. If interactions between group size and environmental variables were nonsignificant for all four of the models, then these interactions were removed from the models; if group size on its own was also nonsignificant in all four models, then this was removed as well. These five models (including the null model) were then compared using AIC. During our model selection process, we chose the model with the lowest AIC value unless there was a simpler model with two AIC points lower than the best model. The best of these five models was then moved forward to the next stage where it was used as a base for investigating the potential effects of short-term changes in environmental variables.

Stage 2: Following the same pattern as the previous set of models, the first model (R1) included short-term changes in rainfall (along with interactions between groups size and short-term changes in rainfall); the second model (R2) included short-term changes in temperature (along with interactions between group size and short-term changes in temperature); the third model (R3) included both short-term changes in rainfall and temperature (along with interactions with group size); the fourth model (R4) was the same as the third model with the addition of an interaction between short-term changes in temperature and rainfall. If interactions between group size and environmental variables were insignificant for all four of the models, then these interactions were removed from the models; if group size on its own was also insignificant in all four models, then this was removed as well. One again we compared these four models along with the best model from the previous set of models using their AIC values to determine the best model.

Stage 3: This model was then moved forward to the final stage where it was used as a base for modelling the potential effects of long-term rainfall and temperature; this followed the same procedure as before (models called T1, T2, T3, and T4). Specific explanations for the modelling of our helping and survival models are described individually below, including any deviations from the general modelling methodology previously explained.

Litter survival to emergence

Each communal litter was determined to have survived (1) or not survived (0) depending on whether at least one pup from the communal litter was found to be alive 30 days from when the litter was born. The proportion of days each litter was babysat by at least one adult (babysitting effort) was calculated as the total number of days the litter was observed being babysat divided by the number of days the litter was observed. After removing litters with fewer than five observations (since measures of babysitting effort is likely to be reliable in these cases) we had a sample size of 449 litters. We modelled litter survival as a function of the environmental conditions from the month of birth, group size at the time the litter was born (and potential interactions between group size and environmental variables) as well as babysitting effort. Initially we fitted group identity as a random effect using a binomial GLMM however the variance of the random effect was zero, so this was removed and a binomial GLM was used instead.

Babysitting effort

Using the same set of litters that we used to analysis litter survival to emergence from the den (30 days), we investigated the probability of a communal litter being babysat using a binomial GLMM with environmental conditions and group size, as well as interactions between them, as explanatory variables. Initially we fitted group identity as a random factor, however the model was overdispersed (1.86). In order to deal with this overdispersion, we used an observation level random effect (OLRE) (Harrison 2015). When running these models, the response variable (proportion of days spent babysitting) was weighted by the total number of days the litter was observed since this varied between litters (5-35 observations) (Bates *et al.* 2015) .

Pup survival to independence

For each pup that emerged from the den (at 30 days old), survival to nutritional independence (90 days) was then determined; survived (1) or did not survive (0). Survival was modelled as our response variable, with the proportion of time each pup was escorted, the environmental conditions, group size at the time of emergence (and interactions between group size and environmental conditions) as explanatory variables. We calculated the proportion of days each pup was escorted (escorting effort) as the number of days the pup was observed being escorted divided by the total number of days it was observed. This model was fit as a binomial GLMM with group identity as a random effect. After excluding any pups that were observed fewer than five times, we had a sample size of 740 pups.

Escorting effort

Using the same dataset as for our survival to independence model (90 days), we investigated how environmental conditions and group size, including interactions between the two, affects the proportion of time each pup is escorted. This was done using a binomial GLM with group identity being excluded as a random effect and an OLRE being used instead in order to accommodate the overdispersion (2.03). When running these models, the response variable (proportion of sessions the pup was escorted) was weighted by the total number of days the litter was observed since this varied between groups (5-37).

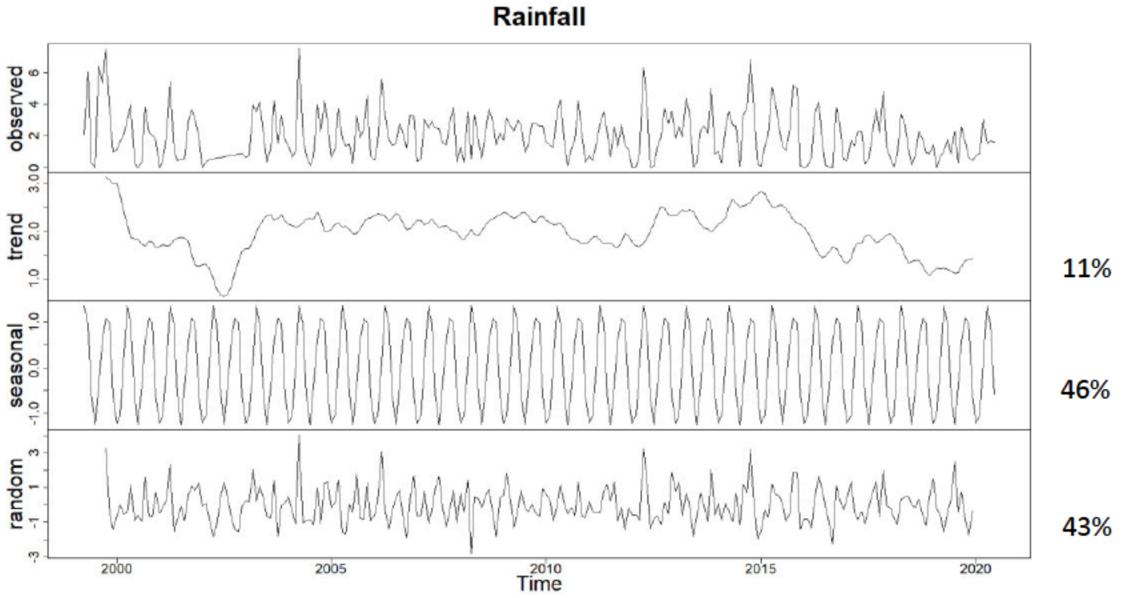
Checking for time-lags

It is possible that lags could be present in the effect of our environmental conditions on helping and/or survival. This might be expected if, for example, high levels of rainfall in one month leads to greater invertebrate abundance the following month or if environmental conditions during pregnancy influence survival of offspring. To investigate this possibility, we repeated our modelling process using the environmental conditions from the previous month. However, after comparing AIC values, we found no evidence of environmental conditions a month prior being a better predictor of our response variables (helping behaviour or survival).

Decomposition output

Rainfall varied considerably over time, ranging from an average of 0 to 7.51 mm per day over each month. Our decompositions showed that seasonal variation explained a large percentage of variance (46%) in the observed average monthly rainfall (Fig S1a); with two distinct peaks in seasonal rainfall per year, one lower but longer lasting (the long-wet season) and another higher but short lived (the short-wet season) (Fig S1a). Long-term changes explained relatively little variance (11%) in rainfall, while short-term changes explained 43% of variance, demonstrating that rainfall often fluctuates over short timescales.

Temperatures remained relatively constant over time, with our observed average monthly maximum temperatures varying from 25.68 to 34.26 °C. Seasonal variation in temperature was lower than for rainfall, explaining 21% of variance (Fig S1b). Long-term changes explained almost half (48%) of the variation in the observed monthly maximum temperature while short-term changes explained 31% of the variance in temperature (Fig S1b).



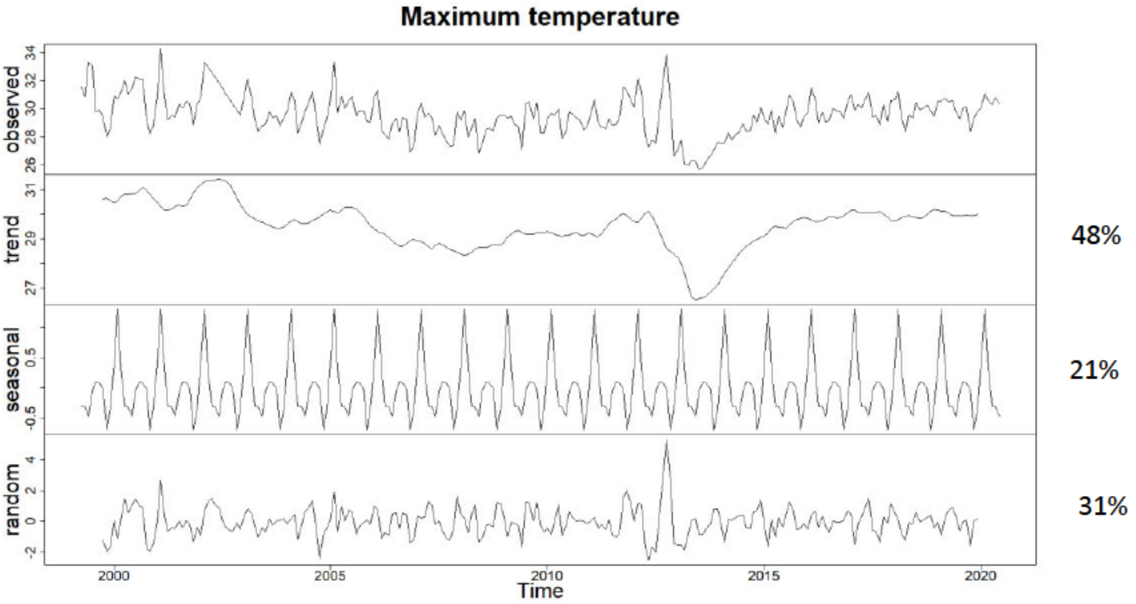


Figure S1. Decomposition output from the mean daily (a) rainfall (mm) and (b) maximum temperature (°C) per month from October 1999 to December 2019 including the long-term changes, seasonal fluctuation, and short-term variation, along with the percent of variance explained by each component. All the components are in the original scale with the exception of seasonality which has been mean-centered by subtracting the average seasonal value from each data point.

3.7.2 Results

Litter survival to 30 days

Table S1: Model comparison table showing the competing models from the pup survival to emergence (~30 days) analysis. This includes the name of the model, the number of parameters (K), logLik (log-likelihood), AIC, deltaAICc (the difference between the best model and every other model), Weight (model probabilities) and Evidence ratio (the amount of evidence for the best model relative to each model i.e. a score of 2 means that there is 2 times less evidence supporting it than the best model). Models with S in their name are from the first stage of the modelling process where only seasonal variables are modelled. Models with R in their name refers to the second stage where short-term changes variation in environmental variables are added. Finally, models with T in their name refers to the final stage where long-term changes in environmental variables are added. The null model contained only group size and group size squared. The final model selected is in bold.

Model	K	logLik	AICc	deltaAICc	Weight	Evidence.ratio
T1	4	-232.91	473.9	0	0.3	1
S2	**3**	**-234.46**	**474.98**	**1.07**	**0.18**	**1.71**
T3	5	-232.73	475.59	1.68	0.13	2.32
R2	8	-230.04	476.4	2.5	0.09	3.49
T2	4	-234.4	476.89	2.98	0.07	4.45
S3	4	-234.4	476.89	2.99	0.07	4.46
T4	6	-232.62	477.44	3.53	0.05	5.85
S4	5	-233.98	478.1	4.19	0.04	8.14
R3	11	-227.8	478.2	4.3	0.04	8.56
S1	3	-236.96	479.98	6.08	0.01	20.86
R4	12	-227.74	480.2	6.3	0.01	23.28
R1	8	-232.78	481.89	7.99	0.01	54.34
Null	4	-237.8	483.69	9.79	0	133.48

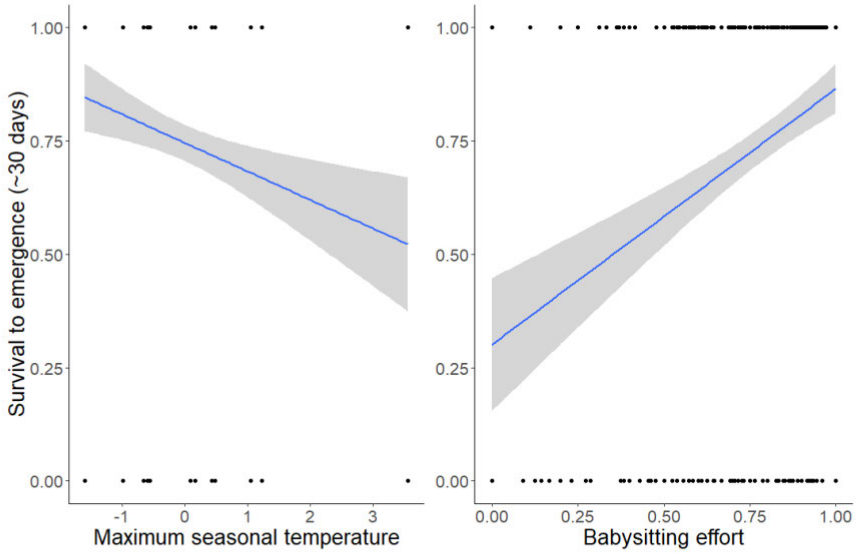


Figure S2. The probability of litters surviving to emergence (30 days) as a function of (a) fluctuating maximum seasonal temperatures and (b) the proportion of time the litter was babysat. Trend lines were fitted based on a GLM relationship with the shaded regions showing the 95% confidence interval.

Babysitting effort

Table S2: Model comparison table showing the competing models from the babysitting effort analysis. This includes the name of the model, the number of parameters (K), logLik (log-likelihood), AIC, deltaAICc (the difference between the best model and every other model), Weight (model probabilities) and Evidence ratio (the amount of evidence for the best model relative to each model i.e. a score of 2 means that there is 2 times less evidence supporting it than the best model). Models with S in their name are from the first stage of the modelling process where only seasonal variables are modelled. Models with R in their name refers to the second stage where short-term changes variation in environmental variables are added. Finally models with T in their name refers to the final stage where long-term changes in environmental variables are added. The null model contained only group size and group size squared. The final model selected is in bold.

Model	K	logLik	AICc	deltaAICc	Weight	Evidence.ratio
T4	7	-969.99	1954.23	0	0.53	1
T3	**6**	**-971.59**	**1955.36**	**1.14**	**0.3**	**1.77**
T1	5	-973.23	1956.6	2.37	0.16	3.27
S1	4	-979.09	1966.26	12.04	0	411.01
R3	8	-975.17	1966.67	12.44	0	502.74
R2	6	-977.25	1966.68	12.46	0	506.52
R1	6	-977.25	1966.68	12.46	0	507.07
S3	5	-978.93	1967.99	13.77	0	975.52
T2	5	-979.08	1968.29	14.06	0	1132.14
S4	6	-978.22	1968.64	14.41	0	1346.99
R4	12	-972.6	1969.91	15.68	0	2543.95
S2	4	-983.21	1974.52	20.29	0	25493.98
Null	4	-983.22	1974.54	20.31	0	25728.53

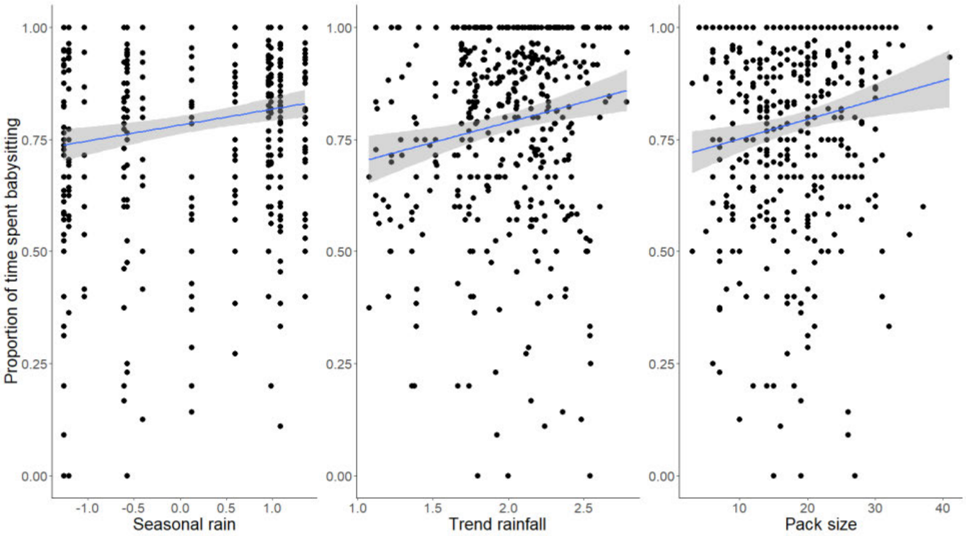


Figure S3. The proportion of time a litter was babysat (babysitting effort) as a function of (a) seasonal fluctuations rainfall, (b) long-term changes in rainfall and (c) group size. Trend lines were fitted based on a GLM relationship with the shaded regions showing the 95% confidence interval.

Survival to 90 days

Table S3. Model comparison table showing the competing models from the pup survival to independence (90 days) analysis. This includes the name of the model, the number of parameters (K), logLik (log-likelihood), AIC, deltaAICc (the difference between the best model and every other model), Weight (model probabilities) and Evidence ratio (the amount of evidence for the best model relative to each model i.e. a score of 2 means that there is 2 times less evidence supporting it than the best model). Models with S in their name are from the first stage of the modelling process where only seasonal variables are modelled. Models with R in their name refers to the second stage where short-term changes variation in environmental variables are added. Finally models with T in their name refers to the final stage where long-term changes in environmental variables are added. The null model contained only group size and group size squared. The final model selected is in bold.

Model	K	logLik	AICc	deltaAICc	Weight	Evidence ratio
T2	**21**	**-390.05**	**823.38**	**0**	**0.66**	**1**
R4	19	-393.77	826.59	3.21	0.13	4.98
T3	24	-389.35	828.38	5	0.05	12.21
R3	18	-395.76	828.48	5.1	0.05	12.79
R1	15	-399.31	829.29	5.91	0.03	19.22
T4	25	-388.78	829.38	6	0.03	20.13
R2	15	-400	830.66	7.28	0.02	38.15
T1	21	-394.37	832.03	8.65	0.01	75.57
S4	12	-405.22	834.87	11.5	0	313.47
S3	11	-407.67	837.71	14.33	0	1291.36
S2	8	-415.18	846.56	23.18	0	107834.48
S1	8	-419.47	855.14	31.76	0	7875032.59
Null	5	-428.15	866.38	43	0	2177004990.09

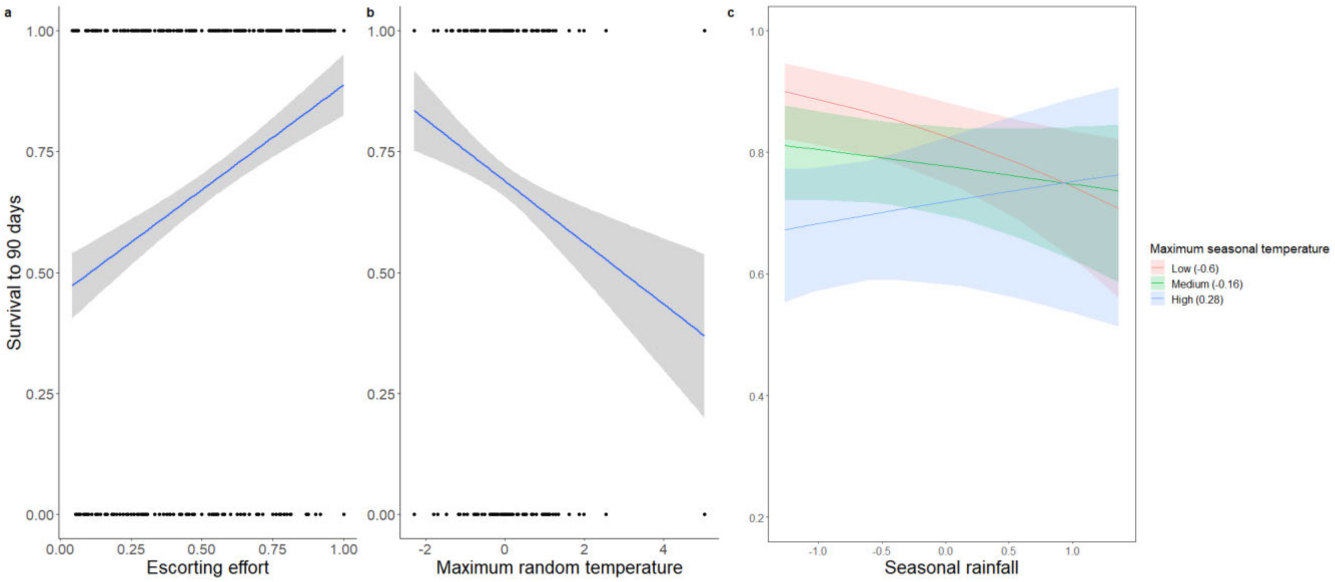


Figure S4. The probability of a pup surviving to 90 days as a function of (a) the proportion of time the pup was escorted (escorting effort) and (b) short-term changes variation in the maximum temperature (residual variation left after long-term changes and seasonal fluctuations have been accounted for). Trend lines were fitted along with shaded regions showing the 95% confidence interval. The probability of survival is also plotted as a function of (c) the interaction between maximum seasonal temperature and seasonal rain with data points overlayed onto the heat map; red represent a high probability of pup survival whereas blue represents a low probability.

Escorting effort

Table S4. Model comparison table showing the competing models from the escorting effort analysis. This includes the name of the model, the number of parameters (K), logLik (log-likelihood), AIC, deltaAICc (the difference between the best model and every other model), Weight (model probabilities) and Evidence ratio (the amount of evidence for the best model relative to each model i.e. a score of 2 means that there is 2 times less evidence supporting it than the best model). Models with S in their name are from the first stage of the modelling process where only seasonal variables are modelled. Models with R in their name refers to the second stage where short-term changes variation in environmental variables are added. Finally models with T in their name refers to the final stage where long-term changes in environmental variables are added. The null model contained only group size and group size squared. The final model selected is in bold.

Models	K	logLik	AICc	deltaAICc	Weight	Evidence.ratio
T2	**11**	**-1848.43**	**3719.23**	**0**	**0.36**	**1**
T4	13	-1846.71	3719.93	0.7	0.25	1.42
T3	12	-1848.26	3720.96	1.73	0.15	2.37
R2	10	-1850.77	3721.85	2.62	0.1	3.7
R3	13	-1848.48	3723.46	4.23	0.04	8.29
T1	11	-1850.65	3723.66	4.43	0.04	9.18
R4	14	-1848.01	3724.61	5.38	0.02	14.7
S3	10	-1853.22	3726.75	7.52	0.01	42.93
S1	7	-1856.45	3727.05	7.82	0.01	49.89
R1	10	-1853.6	3727.49	8.26	0.01	62.2
S4	11	-1852.85	3728.06	8.83	0	82.66
Null	4	-1863.04	3734.13	14.9	0	1716.03
S2	7	-1861.52	3737.2	17.97	0	7975.92

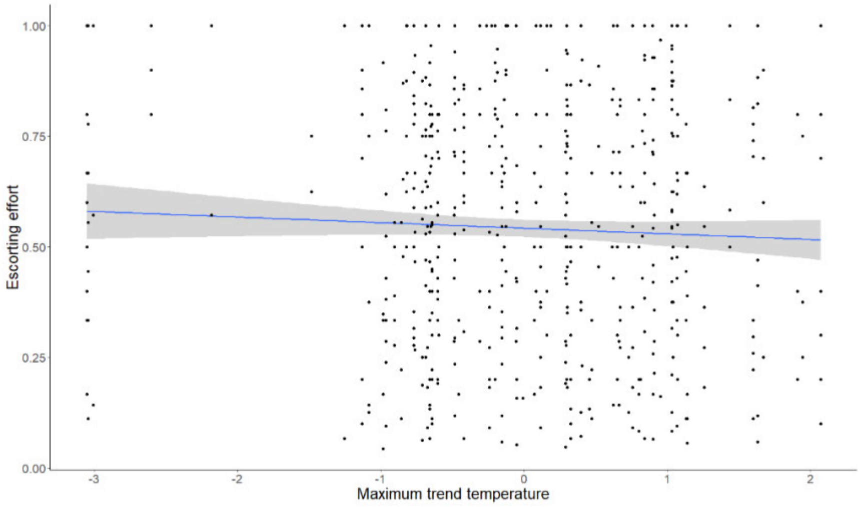


Figure S5. The proportion of time a pup was escorted (escorting effort) as a function of the changes in the long-term maximum temperature. Trend lines were fitted based on a GLM relationship with the shaded regions showing the 95% confidence interval.

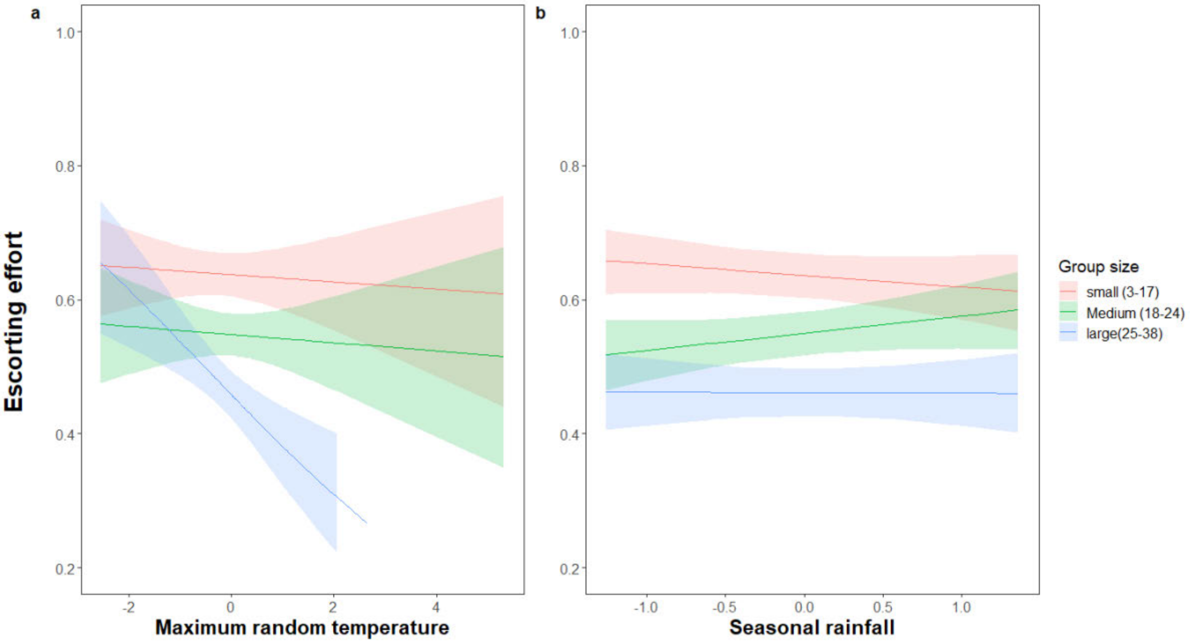


Figure S6. The probability of a pup being escorting as a function of the interaction between group size and (a) short-term variation in temperatures (residual variation left after long-term changes and seasonal fluctuations have been accounted for) and (b) seasonal rainfall.

Table S5. Marginal and conditional R^2 values used to indicate the proportion of variance in the response terms explained by the fixed or fixed and random effects.

Response	Marginal R^2	Conditional R^2
Litter survival to emergence (30 days)	0.13	NA
Babysitting probability	0.02	0.15
Pup survival to independence (90 days)	0.21	0.24
Escorting probability	0.03	0.26

Table S6. Independence claims from my piecewise structural equation models. The first column indicates which structural equation model the independence claim is from, this is followed by the independence claim where the first variable is the response, and the second variable after the ~ is the explanatory variable.

SEM	Independence claim	d.f.	critical value	*p*-value
1	Babysitting effort ~ Maximum seasonal temperature	445	-0.5912	0.5544
1	Survival to emergence (30 days) ~ Seasonal rainfall	445	0.3458	0.7295
1	Survival to emergence (30 days) ~ Group size	445	0.1572	0.8751
1	Survival to emergence (30 days) ~ Long-term rainfall	445	-1.7445	0.08
2	Escorting effort ~ Maximum seasonal rain	740	1.0255	0.3051
2	Escorting effort ~ Short-term rainfall	740	1.3519	0.1764

4 Small increases in ambient temperature reduce offspring body mass in an equatorial mammal

Accepted for publication in Biology Letters.

4.1 Abstract

Human-induced climate change is leading to temperature rises, along with increases in the frequency and intensity of heatwaves. Many animals respond to high temperatures through behavioural thermoregulation, for example by resting in the shade, but this may impose opportunity costs by reducing foraging time (therefore energy supply), and so may be most effective when food is abundant. However, the heat dissipation limit theory (HDL) proposes that even when energy supply is plentiful, high temperatures can still have negative effects. This is because dissipating excess heat becomes harder, which limits processes that generate heat such as lactation. We tested predictions from HDL on a wild, equatorial population of banded mongooses (*Mungos mungo*). In support of HDL, higher ambient temperatures led to lighter pups, and increasing levels of rainfall (a proxy for food availability) made little difference to pup weight under hotter conditions. This suggests that direct physiological constraints rather than opportunity costs of behavioural thermoregulation explain the negative impact of high temperatures on pup growth. Our results indicate that climate change may be particularly important for equatorial species, which often experience high temperatures year-round so cannot time reproduction to coincide with cooler conditions.

Key words: Heat dissipation limit theory, climate change, equatorial, thermoregulation, banded mongoose, cooperative breeder

4.2 Introduction

Human-induced climate change is causing average temperatures to rise and is increasing the frequency, severity, and duration of heatwaves (Meehl & Tebaldi 2004). High temperatures have been shown to negatively impact a variety of key mammalian life-history traits including body size, reproductive success, and survival, which may in turn lead to population declines (Walther *et al.* 2002; Williams & Tieleman 2005; Bourne *et al.* 2020a; Rabaiotti *et al.* 2022). Many species attempt to avoid hyperthermia by changing their behaviour, for example through a reduction in activity or microhabitat selection of cooler locations (Wolf & Walsberg 1996; Lopes & Bicca-Marques 2017). However, these strategies, collectively called 'behavioural thermoregulation', can be costly in terms of lost opportunities because they require animals to alter their patterns of behaviour, which can carry significant fitness costs. For example, animals may cease foraging during hot periods, which can reduce their energy intake (Aublet *et al.* 2009).

High temperatures may also be costly, even when there is ample food available from the environment (Porter *et al.* 1994). The heat dissipation limit (HDL) theory proposed by Speakman et al. (Speakman & Król 2010) suggests that that as air temperature increases, it becomes harder for metabolic heat to be lost, and if heat is generated faster than it can be lost, this will cause hyperthermia. The reduced capacity for heat to be dissipated (rather than energy availability) may therefore be the primary limiter of maximum energy expenditure (Speakman & Król 2010).

Lactation is considered the most energetically costly event in a female mammal's lifetime (Król *et al.* 2007), and milk production is a highly exothermic process (Król & Speakman 2003b, a), leading to lactating animals being particularly vulnerable to chronic hyperthermia (Speakman & Król 2005). In support of the HDL theory, experimental studies on captive mice (*Mus musculus*) (Johnson & Speakman 2001; Król & Speakman 2003b), pigs (*Sus scrofa domesticus*) (Renaudeau & Noblet 2001), dairy cattle (*Bos taurus*) (Igono *et al.* 1992) and hamsters (*Cricetulus barabensis*) (Zhao *et al.* 2020) have found high temperatures to depress milk production and reduce offspring growth, although it is unclear from these studies whether females stop lactating before or after mild hyperthermia sets in. The HDL theory has also been supported by multiple fur-removal experiments (Król *et al.* 2007; Szafranska *et al.* 2014; Sadowska *et al.* 2016; Ohrnberger *et al.* 2020), whereby removing fur increases thermal conductance, allowing for greater heat dissipating capacity.

So far, the HDL theory has been predominantly tested via laboratory experiments, with very few studies testing the HDL theory in the wild (but see Nilsson et al. (Nilsson & Nord 2018) who studied HDL in relation to brood care in birds, rather than lactation in mammals). When studies have been conducted in captivity, food is given *ad libitum*, such that the HDL theory in relation to lactation remains untested under limited food resources. In natural systems, food supply largely determines energy availability and can have a strong impact on reproductive output (Simons *et al.* 2011), so studies of wild systems are required to understand the relative importance of high temperatures and food supply on lactation and offspring growth (Simons *et al.* 2011).

There is also a lack of studies investigating the impact of high temperatures in equatorial species. Animals living close to the equator at low altitudes experience relatively high temperatures year-round with little seasonal variation compared to those in temperate regions. Equatorial species are therefore likely to be physiologically adapted to relatively constant temperatures, and so may have narrow thermal ranges which could leave them particularly susceptible to even small changes in temperatures (Janzen 1967; Wright *et al.* 2009). Furthermore, in temperate regions, high seasonal temperatures are generally associated with an increase in food availability (McNutt *et al.* 2019) which can make it difficult to distinguish between the direct effect of temperature on reproductive output versus indirect effects via impacts on food supply (Simons *et al.* 2011). Tropical regions, however, are characterised by high seasonal variation in rainfall, which is often the main determinant of food supply (Wolda 1978; Dangerfield & Telford 1991; Poulin *et al.* 1992; Bronson 2009). Studying equatorial species can therefore allow us to decouple the impacts of temperature variation and food supply on energy dynamics.

Here, we test the HDL theory in a wild population of banded mongooses (*Mungos mungo*) in equatorial Uganda. Banded mongooses live in family groups where females (mean = 3.5 females, range 1 to 13) give birth synchronously (usually on the same night) to between 1-5 pups each (Cant 2000). The resultant litters are raised communally in an underground den, and pups are suckled indiscriminately by multiple lactating females for approximately 30 days before the weaning process begins (Cant 2000; Hodge *et al.* 2011). Underground rearing is likely to buffer pups against direct negative effects of high temperatures (Pike & Mitchell 2013), therefore separating thermal effects on pups from those on lactating females. This makes them ideal for studying the indirect effects of high temperatures on pup growth via its effect on milk production. Furthermore, banded mongoose adults behaviourally thermoregulate by foraging when temperatures are cooler, resting in the shade during the hottest parts of the day (Cant *et al.* 2013). High temperatures therefore likely result in reduced time available for foraging (Chapter 5). However, rainfall is tightly linked to the availability of invertebrate prey (Rood 1975; De Luca 1998; Marshall *et al.* 2017), allowing us to investigate whether high food availability can compensate for the negative impacts of high temperatures.

4.3 Methods

Our study used life history, body mass, genetic, and environmental data collected between August 2000 and March 2018 from a population of wild banded mongooses in Queen Elizabeth National Park, Uganda (0° 12'S, 27° 54'E). At any one time, the population was made up of 8-12 social groups, each of which typically contained between 10-30 adults (Cant *et al.* 2016). Banded mongooses primarily feed on invertebrates (Gilchrist *et al.* 2004) and whilst groups forage together, foraging itself is not cooperative (De Luca & Ginsberg 2001). Groups undertook two foraging sessions per day; the first session beginning shortly after dawn and usually lasting between three to four hours, and the second session beginning in the afternoon, usually lasting two to three hours and finishing before sunset (Cant *et al.* 2013; Chapter 5).

4.3.1 Climatic variables

Our study site is located in a scrub-savannah habitat and can be characterised by relatively constant temperatures (monthly mean maximum daily temperature ± SD = 29.5 ± 1.5 °C) (Marshall *et al.* 2016). Nevertheless, short-term variation does occur, including heatwaves (Amondo *et al.* 2021). There are also two rainy seasons per year, from March-May and August-December, with drier periods in between. We used rainfall as a proxy for food availability as invertebrate prey are more abundant at higher rainfall (Rood 1975; De Luca 1998), and rainfall has previously been shown to positively affect weight gain in adults (Marshall *et al.* 2016) and pups (Nichols *et al.* 2012b). Data on rainfall (mm) and maximum ambient temperature (Tmax) (°C), both measured to 1 decimal place, were collected daily from a weather station located in our study site.

4.3.2 Life history

Our study population is habituated to observation at <10m (usually <5m) (Jordan *et al.* 2010). Each social group was visited every 1-3 days to determine group composition and record births, deaths, and other life-history data (Thompson *et al.* 2017). Pregnancies and births were identified by changes in the size and shape of the abdomen, the absence of previously pregnant females on foraging trips the morning after birth, and the start of pup-care behaviour (Cant 2000; Gilchrist 2006a; Cant *et al.* 2016).

4.3.3 Body mass

Since pups are raised in underground dens it was not possible to weigh them until they emerged at approximately 30 days old, after which they start accompanying the group on foraging trips and wean onto solid food (Cant *et al.* 2016). Pups were caught by hand, sexed and weighed using a portable electronic scale (accuracy ±1.5 g) in the morning (ca 7:30AM) (see Jordan et al. (Jordan *et al.* 2010)). Due to time constraints and field researcher safety considerations, there was some variation in the age of pups at first weighing. This study included 215 pups weighed when they were between 28 and 38 days old (mean mass = 188.9g (range 87- 307g); mean age at weighing = 32.9 days), which captures an age range at which weighing pups is possible but when pups still rely heavily on milk.

4.3.4 Maternity

Synchronised birthing masks the maternity of banded mongoose pups so maternity cannot be determined behaviourally. Instead, maternity data was extracted from an existing genetic pedigree based on 35-43 microsatellite loci; see (Sanderson *et al.* 2015c) and (Wells *et al.* 2018).

4.3.5 Statistical analysis

We constructed a linear mixed effects model (LMM) in R version 4.2.1 (R Core Team 2022), with pup mass as our response variable. To investigate how rainfall affected pup mass at varying temperatures, we modelled the interaction between rainfall and temperature. We used mean daily Tmax (°C) during the lactation period (0-30 days) and the mean rainfall (mm) over the 30 days prior to the birth of the pup as a proxy for food availability during the lactation period, since it takes this time for high rainfall to translate into higher food availability (Rood 1975; De Luca 1998; Marshall *et al.* 2017). Previous studies also indicate that rainfall over this time period is positively correlated with adult daily weight gain (Marshall *et al.* 2016). In our model, mean Tmax ranged from 27.0 – 32.1°C and mean rainfall values ranged from 0.1 to 6.5mm. Our rainfall and temperature measures were not strongly correlated (correlation coefficient = 0.081). The number of lactating females present in the group was added as a covariate since pups with access to more lactating females may be able to obtain more milk, although these pups will likely also face higher competition from other pups. Sex was fitted as a covariate since male pups were previously found to weigh slightly more than females (Vitikainen *et al.* 2017), and pup age was included to account for age differences in weighing. It is possible that offspring weight might vary by mother (Russell *et al.* 2003a) so we fitted the identity of the mother as a random effect. We also fitted the identity of the social group as a random effect to account for variation in group-level factors such as territory quality. Standard model checks were employed following Crawley (2015).

4.4 Results

Pup mass was significantly affected by the interaction between temperature and rainfall (Table 1). Under cooler temperatures, higher levels of rainfall were associated with heavier pups, however, under hotter conditions, changes in rainfall had little effect on pup mass (Fig 1). Our model controlled for the significant effect of pup age at weighing, and we found no effect of pup sex or the number of lactating females.

Table 1. Summary of an LMM investigating pup mass after the lactation period. Our model included 215 pups, with 60 different mothers, born into nine social groups.

Fixed effects	Estimate	SE	d.f.	t-value	P-value
Intercept	-269.983	135.505	191	-1.99	0.0477
Age	3.132	0.884	198	3.55	4.90x10^{-4}
Sex (Male)	5.986	4.506	182	1.33	0.186
Number of lactating females	-1.598	1.343	194	-1.19	0.235
Rainfall	170.137	42.966	188		
Temperature	11.712	4.649	191		
Temperature: Rainfall	-5.574	1.458	187	-3.82	1.79x10^{-4}

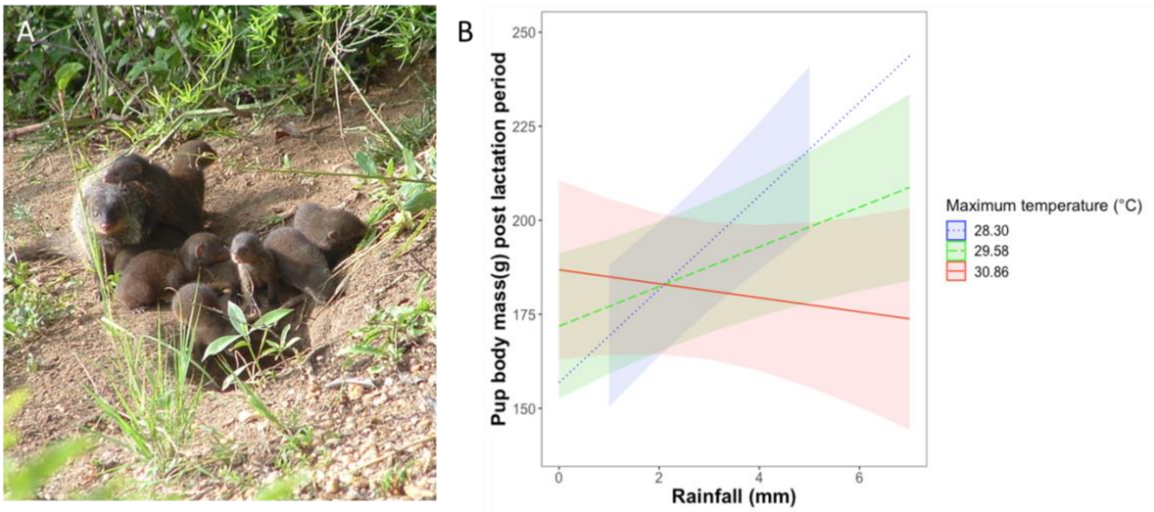


Figure 1. A) Banded mongoose pups emerging from their underground den at around 30 days old. B) Pup body mass as a function of the interaction between temperature and rainfall. Lines show the predictions from the LMM, plotted for three temperatures; 28.3 (mean-1SD), 29.6 (mean), and 30.9 °C (mean+1SD), with the shaded areas representing 95%CI. Temperature was included as a continuous variable in our analysis, but we show the predicted rainfall-pup mass relationship at three temperatures for illustrative purposes. At low and medium temperatures, pup weight increases with rainfall, however at high temperatures, there is no effect of rainfall on pup weight (as evident from the CIs).

4.5 Discussion

We found that under hotter conditions, increased rainfall (a proxy for food availability) did not lead to increased banded mongoose pup mass. This is consistent with the heat dissipation limit (HDL) theory, which proposes that as the air temperature gets closer to body temperature, dissipating heat becomes harder (Speakman & Król 2010). As a result, lactating females may be forced to suppress exothermic processes such as milk production (either at or approaching their critical thermal maximum) in order to avoid hyperthermia (Johnson & Speakman 2001). At lower ambient temperatures, however, banded mongoose pup body mass increased with rainfall (a proxy for food supply). Here, heat dissipation can happen faster, which may lift constraints on how quickly energy can be metabolised (Speakman & Król 2010). As a result, when there is sufficient food available, females can consume more energy to increase milk production, which is consistent with our finding of greater pup growth.

In addition to placing constraints on lactation, high temperatures could also directly affect the pups' ability to dissipate heat causing them to reduce milk intake in order to avoid hyperthermia, although likely to a lesser extent than adults due to the pups' higher surface area to volume ratios (Simons *et al.* 2011). Similar effects have been found in meerkats, whereby weaned pups have reduced mass gain at high temperatures, but without an apparent reduction in feeding rate (Van de Ven *et al.* 2020). However, in our study of banded mongooses, we focused on pups that are raised in underground dens pre-weaning. Whilst there have been no studies of the thermal properties of banded mongoose dens, similar structures have been shown to provide insulation against temperature fluctuations in a variety of other species (Bennett *et al.* 1988; Williams *et al.* 1999; Roper *et al.* 2001). Dens are therefore likely to provide protection to banded mongoose pups against direct negative effects of high temperatures. Lactating females, however, must forage in ambient temperatures, thus limitations on lactation are likely to produce the greatest impacts on pup growth in this species.

High temperatures during the lactation period are likely to have downstream impacts on pups post-weaning. For example, pups that are lighter at emergence from the den are less likely to survive to nutritional independence (90 days) (Nichols *et al.* 2012b; Vitikainen *et al.* 2019) and weigh less at maturity (1 year) (Vitikainen *et al.* 2019). Furthermore, body mass at maturity influences lifetime reproductive success, with lighter individuals of both sexes producing fewer pups (Vitikainen *et al.* 2019). Hot conditions experienced in early-life could therefore have lifelong fitness implications.

High temperatures are also likely to have impacts that go beyond body mass. For example, high seasonal temperatures have been shown to reduce the probability of the communal litter surviving to 30 days (Chapter 3). As our findings are based on those pups that survived the lactation period, we may have missed cases where lactation has been reduced to the extent that it has caused pup mortality prior to the emergence of the litter from the den. Unfortunately, it is rarely possible to observe or weigh banded mongoose pups while in the den, so causes of pre-emergence mortality are difficult to determine.

High temperatures during the early developmental stages have also been found to negatively impact other species. For example, hot conditions reduce the survival of southern pied babblers (*Turdoides bicolor*) to independence (Bourne *et al.* 2020a), reduce mass gain and fledgling mass in common fiscal nestlings (*Lanius collaris*) (Cunningham *et al.* 2013) and reduce mass gain and weight at nutritional independence in meerkats (Van de Ven *et al.* 2020). Reduced body size is in turn associated with reduced survival, fecundity, and reproductive success (Magrath 1991; Haywood & Perrins 1992; Green & Cockburn 2001). Therefore, the negative impacts of hot conditions during development on lifelong fitness could be relatively common amongst birds and mammals, although the importance of HDL across species is currently unclear and needs testing.

As global temperatures rise and heatwaves increase in frequency and intensity (Meehl & Tebaldi 2004), temperate species may be able to adjust their reproductive phenology (Réale *et al.* 2003; Moyes *et al.* 2011), for example to avoid lactating when seasonal temperatures are high. It is unclear, however, if and how equatorial species will be able to adapt to these changes. Our study confirms the susceptibility of an equatorial species to small changes in temperature; mean daily maximum temperatures over the lactation period only ranged from 27.0 to 32.1°C. Our results also imply that high food abundance may not compensate for the negative impacts of high temperatures on lactating females. Although rainfall is predicted to increase in western Uganda with climate change (Diem *et al.* 2019a), temperatures across Uganda are also continuing to rise (Babel & Turyatunga 2015) and so over time, increased rainfall may not compensate for higher temperatures, and rainfall may cease to predict pup mass. In light of rising global temperatures as well as more intense and frequent heatwaves (Meehl & Tebaldi 2004), we highlight a clear need for greater research efforts on the effect of climatic variation on species occupying tropical and equatorial regions, where populations live and breed under consistently high temperatures.

Acknowledgements: We thank Uganda Wildlife Authority and Uganda Council for Science and Technology for permission to conduct our research, and the wardens of Queen Elizabeth National Park for support with our long-term study. We are very grateful to the Uganda field team, and past and present researchers for the long-term data collection. We also thank David Wells for his help and advice on generating the pedigree.

Funding: This work was supported by the Natural Environment Research Council [grant reference: NE/N011171/1] and the European Research Council [grant reference: 309249]. HJN was supported by an Alexander von Humboldt Foundation Research Fellowship.

5 High ambient temperatures constrain foraging ability in an equatorial mammal

5.1 Abstract

Under high ambient temperatures, animals often use behavioural thermoregulation to avoid potentially dangerous hyperthermia, for example they may become less active and rest in the shade. However, this can result in trade-offs with other important activities such as foraging, reproduction and social behaviours. We studied a wild population of cooperatively breeding banded mongooses (*Mungos mungo*) in Uganda to determine 1) whether behavioural thermoregulation occurs and 2) whether it is sufficient to maintain stable body surface temperatures in light of changing ambient temperatures. We found that banded mongooses respond to increasing ambient temperatures by reducing activity levels; foraging less and resting more. Foraging ability is therefore likely to be constrained at high temperatures. This may explain why previous studies have found that offspring care is reduced under high temperatures, resulting in lower pup survival, as adults may struggle to meet their daily food requirements and prioritise their own survival over helping raise pups. Our results also show that body surface temperatures increase with rising ambient temperatures, suggesting that behavioural thermoregulation may not be sufficient to buffer them against rising temperatures. As global temperatures continue to rise, lowland equatorial species (which are already subject to high ambient temperatures) may struggle to behaviourally thermoregulate and maintain energy intake through foraging. Our study highlights that fine-scale quantification of behaviours in wild systems is important for understanding the mechanisms underlying the effect of changing environmental conditions on natural populations.

5.2 Introduction

Human-induced climate change is leading to increased average temperatures and thermal extremes (Donat & Alexander 2012; Lee *et al.* 2021). This will likely lead to difficulty in thermoregulation for many species, which may result in dangerous hyperthermia (Lovegrove *et al.* 2014; Conradie *et al.* 2020), reduced body condition (Gardner *et al.* 2016; Sharpe *et al.* 2019), increased mortality (McKechnie & Wolf 2010; Bourne *et al.* 2020a, b), and impaired reproduction (McNutt *et al.* 2019). Animals may be able to reduce some of the costs of being exposed to high ambient temperatures by changing their behaviours, a strategy known as 'behavioural thermoregulation' (Terrien *et al.* 2011). Understanding the extent to which behaviours can help to mitigate against harsh conditions is important when estimating the impact of climate change on extinction risk (Enriquez-Urzelai *et al.* 2020).

The most widespread form of behavioural thermoregulation is to minimise heat gain from the environment by avoiding locations with high temperatures (Wolf & Walsberg 1996; Giotto *et al.* 2013; Lopes & Bicca-Marques 2017). Similarly, reducing activity levels minimises metabolic heat production, which can also minimise heat gain (Cain III *et al.* 2006). This can result in bimodal activity patterns, with many animals from hot regions being most active in the mornings and evenings and resting in the shade during the hotter parts of the day (Carmi-Winkler *et al.* 1987; Hinsley 1994; Williams 2001). For example, high temperatures have been shown to reduce foraging behaviour of the alpine ibex (*Capra ibex*) during the mid-day (Aublet *et al.* 2009).

Whilst some thermoregulatory behaviours reduce heat gain, others increase heat loss. For example, wallowing or covering the body in mud or water increases conductive and evaporative heat loss in large mammals (McKay 1973; Mota-Rojas *et al.* 2021). Panting or otherwise exposing mucous membranes to the air can also be an effective way to cool through evaporative heat loss (Dawson 1982; Loughran & Wolf 2023). This strategy is most effective in low humidity because evaporative cooling requires body water vapour to move into the surrounding air across a humidity gradient, such that the rate of evaporative heat loss is directly related to the difference in humidity between the surface of the animal and the environment (Powers 1992; Gerson *et al.* 2014; Mitchell *et al.* 2018). High wind speeds allow the humidity gradient to be sustained by moving the accumulating water vapour away from the body surface during evaporative cooling, again improving its efficiency (Mitchell *et al.* 2018). Finally, animals may reduce physical contact with each other at high temperatures, as maintaining close contact can reduce surface area exposed to lower temperatures and impair cooling, in addition to increase contact with body heat of other individuals (Gilbert *et al.* 2010).

Although behavioural thermoregulation can be effective, the strategies used can often incur a fitness cost. For example, reducing activity and resting in the shade during hot periods can lead to lost opportunities for foraging, and may lead to reduced energy intake and lower body condition (Aublet *et al.* 2009). This is seen in the southern yellow-billed hornbills (*Tockus leucomelas*) where thermoregulation under hot conditions via panting behaviour and selecting cooler microhabitats results in a reduction in foraging efficiency with negative consequences for body condition (Van de Ven *et al.* 2019). Behavioural thermoregulation may also place constraints on social behaviour, for example, a reduction in physical contact between individuals may constrain social bonding behaviours such as grooming, although contact between individuals can potentially create shade and hence reduce exposure to solar radiation (Cain III *et al.* 2006).

Thermoregulation may pose a particular problem for species living in the tropics where external temperatures are close to their thermal tolerance limits (Deutsch 2008; Sinervo *et al.* 2010). This makes them more likely to experience conditions conducive to heat stress (West 2003). Furthermore, since tropical lowland species are adapted to living under narrow temperature ranges, they should be disproportionately vulnerable to even small increases in temperature (Tewksbury *et al.* 2008; Bozinovic 2011). Despite this, most previous studies on the behavioural responses of mammals to climate change have focused on temperate or subtropical regions with equatorial mammals receiving little attention.

Banded mongooses (*Mungos mungo*) present an excellent opportunity to study fine-scale behavioural changes in response to temperature. Equatorial populations of this species experience little seasonal variation in temperature, but short-term temperature variation is considerable, allowing us to compare activity levels and behaviour under a relatively large range of temperatures. Though no formal study has been conducted, anecdotal observations over ~25 years suggest that banded mongooses display a distinctly bimodal activity pattern, being more active and foraging during the early morning and afternoon and resting during the middle of the day (Rood 1975; Cant *et al.* 2013). This suggests that banded mongooses use behavioural thermoregulation to avoid being active during the hottest parts of the day. However, it remains unknown how effective this is or how body temperature is affected by sex, age, or changes in the external environment. Banded mongooses also engage in huddling behaviour, whereby they aggregate with their bodies touching each other (Gilbert et al. 2010; see also Table 1). It has been suggested that they do this during cooler mornings to prevent heat loss (Rood 1975), however banded mongooses also huddle during the middle of the day (pers obs), suggesting that it may not be associated with retaining heat.

Our study aims to understand how ambient temperature influences banded mongoose behaviour. More specifically we investigate whether behaviour changes in response to changing ambient temperatures. We focus on activity levels, foraging, resting and huddling behaviours, which may all be involved in thermoregulation. We predict that mongooses will become less active under hotter conditions, spending more time resting and less time foraging and huddling. We also investigate whether behavioural thermoregulation is sufficient to keep body surface temperatures stable or whether surface temperatures varies with air temperature and humidity. We predict that body surface temperature will vary with air temperature and humidity as thermoregulation may not be sufficient to dissociate body temperature from air temperature.

5.3 Methods

5.3.1 Study site and population

Our study was conducted from the 7th – 16th May 2023 on a wild social group of 38 banded mongooses residing in Queen Elizabeth National Park, Mweya, Uganda (0° 12'S, 27° 54'E). The group consisted of 24 males and 14 females (aged from 2.5 months to just over 7 years old) which foraged together during the day, either as one large group or sometimes splitting into two smaller subgroups. There were also 12 pups present in the group, which were under 1 month old so were too young to accompany the group on foraging trips and instead remained in the den and were 'babysat' by adults. Babysitters defend the pups from potential predators and attacks from rival groups (Cant *et al.* 2016). Although adults forage in close proximity to each other, each individual forages independently and defends their prey from other individuals (Rood 1975; De Luca & Ginsberg 2001). Banded mongooses primarily feed on a variety of small invertebrates including millipedes, ants, beetles and termites, though they also occasionally eat small vertebrates (Rood 1975) and forage from anthropogenic sources at our study site such as waste bins. Banded mongooses appear to locate prey by smell and, since most of their prey is found in the first ~10cm of soil, they typically use their forepaws to dig up prey (Rood 1975; Cant *et al.* 2013). The territory of the social group studied incorporated a village and safari lodge, from which the mongooses could sometimes forage on anthropogenic food sources, however the majority of foraging time was spent foraging for natural prey. All individuals in the group could be identified by unique 'haircuts' (Hodge 2007; Jordan *et al.* 2010) and were habituated to observers at ~1m, which allowed detailed behavioural and thermal data to be collected.

Our study site is characterised by an equatorial climate with little seasonal change in temperature (monthly mean maximum daily temperature ± SD = 29.5 ± 1.5 °C) (Marshall *et al.* 2016), although temperatures vary during the course of each day, with minimum temperatures typically dipping during the night (mean minimum daily temperature ± SD = 20.2 ± 2.0 °C). Rainfall is characterised by two distinct wet seasons which occur from March-May and August-December (Marshall *et al.* 2016). High rainfall is linked to changes in vegetation and is positively associated with food availability for banded mongooses (Rood 1975; Marshall *et al.* 2017). Our study took place at the end of the March-May wet season when natural food availability was likely to be relatively high.

5.3.2 Data collection

Using a handheld digital camcorder (model B0C249LWG, YinFun), we took 187 focal observations between 7:47 AM and 19:01 PM. Each individual was observed between 1-8 times, though most (33/38) were observed between 4-6 times. We attempted to observe each individual the same number of times, but this was not always possible due to some individuals remaining at the den to babysit and the group sometimes splitting during foraging, leading to some individuals being unavailable for observation. Throughout each focal, we continuously observed the individual's behaviour throughout for an average of 5 minutes, with some variation due to individuals moving out of sight or to areas that we were unable to follow due to safety considerations (range 2 min 21 sec - 6 min 47 sec). We used BORIS software (V.8.19.4 2023-05-29) (Friard & Gamba 2016) to code the behaviours from the videos and calculate the proportion of the focal period the individual spent performing each behaviour using the ethogram in Table 1. Time spent out of sight was excluded from our observations and downstream calculations.

During each focal, we took a humidity (%) and shade temperature (°C) reading, using a digital thermometer and humidity monitor (model 1207, Pitasha) placed on the ground (i.e. at the same level as the mongooses). We recorded wind speed in three categories; no perceptible wind (0), little wind with occasional mild gusts (1) or high wind with frequent or strong gusts (2). Solar radiation could change within seconds and depending on mongoose location, so it was not feasible to collect detailed measurements representing the sun exposure of our focal mongooses. Instead, we recorded it in three categories; fully clouded over (0), partly cloudy (1) or clear sky (2). During each focal, we took a mean of 5 (range 1-14) body surface temperature recordings using a handheld visual infrared thermometer (Model IRO280H, Perfect Prime) from a distance of ~1m. Readings were taken from the head incorporating the eye and ear region, as these areas have little hair and so best represent body surface temperatures (McCafferty *et al.* 2011). We avoided taking temperatures from the nose area as, whilst lacking hair, the nose was often placed in damp or cool areas during foraging, which could result in unrepresentative body surface temperatures. We used the mean body surface temperature (°C) reading per focal in our analyses.

Table 1. Ethogram describing the behaviours performed by banded mongooses (*Mungos mungo*).

Behaviour type	**Behaviour**	**Description**
Active	Walking	The individual uses all four limbs to propel itself forward. The hind limbs are used to produce most of the propulsive thrust whereas the forelimbs are used as struts (Taylor 1970). The head is pointed in the direction of movement.
	Running	The individual uses all four limbs to propel itself forward. There are no more than two feet on the ground at any given time point (Taylor 1970). The head is pointed in the direction of movement.
	Foraging	The individual has its nose to the ground and can be moving or stationary. It can also be eating food or using claws to dig.
	Active socialisation	The individual is interacting with another individual by running towards or away from it, jumping on it or biting it. This is usually in the form of play fighting however occasionally these are serious forms of aggression.
Inactive	Resting	The individual is either lying down with its ventral surface in contact with the ground or sitting with its posterior and hind legs in contact with the ground.
	Huddling	The individual is resting whilst their torso is in contact with at least one other individual. There were at least two other individuals within 0.1m of the focal individual.
	Panting	The individual has its mouth open and is displaying rapid shallow breathing.

5.3.3 Data analysis

All analyses were performed using R version 4.2.1 (R Core Team 2022). To investigate the effect of environmental conditions on behaviour, we constructed a series of four general linear models (GLM's) with a binomial error structure. For each model, the proportion of the focal period spent on one of the following four behavioural categories was fitted as the response variable (1) active (combined data for walking, running, actively socialising with other individuals and foraging), (2) resting, (3) foraging and (4) huddling. Environmental variables (ambient temperature, humidity, sunlight, and wind), and time of day were fitted as explanatory variables. We also included sex and age of the focal individual in the models to control for potential variation related to those attributes (Marshall *et al.* 2016). We did not include the identity of the focal mongoose as a random effect, as preliminary mixed models estimated the variance of this random effect as zero. Time of day was included as a fourth power term to allow for a bimodal activity pattern with two foraging sessions per day (Cant *et al.* 2013). In all models, ambient temperature (°C) and humidity (%) were mean-centred and scaled.

Thermoregulation could be influenced by the temperature gradient between the surface of the body and ambient temperatures (Terrien *et al.* 2011). We therefore repeated our four models with the difference between average body surface temperature and ambient temperature as an explanatory variable, instead of ambient temperature. However, these models all had a higher Akaike Information Criterion (corrected for sample size; AICc) (Johnson & Omland 2004) than models with ambient temperature (ΔAICc ranging from 2.25 to 10.06; Table S1), indicating that using ambient temperature results in better models than using the temperature gradient between the body surface and environment. Standard model checks were employed following Crawley (2015).

To investigate whether behavioural thermoregulation is able to maintain body surface temperatures at a constant level, despite changes in environmental conditions, we constructed a linear mixed effects model (LMM) with mean body surface temperature during the focal as the response variable, and environmental conditions (scaled ambient temperature, scaled humidity, wind and sunlight) along with age and sex fitted as explanatory variables. The identity of the individual focalled was also included as a random effect.

5.4 Results

Ambient temperature and humidity varied substantially over the course of our study, with temperature ranging from 25.3°C (recorded at 8:01am on the 10th May) to 37.2°C (recorded at 2:33pm on the 12th May) (Fig S1) and humidity ranged from 45% to 79%. The most frequently performed behaviour was foraging (mean 54% ± 2.8 of the time budget), followed by resting (21% ± 2.2), huddling (11% ± 2.0), walking (9% ± 0.9), active social behaviour (0.7% ± 0.3), and running (0.5% ± 0.2). Panting was never observed during the course of our data collection.

All of the behaviours we investigated varied non-linearly depending on the time of day. Individuals were more likely to be active and foraging during the morning and afternoon, but were more likely to be resting and huddling in the middle of the day and in the evening (Table 2; Fig 1a-d). After accounting for these daily behavioural changes, banded mongooses were significantly less active, foraged less and rested more under high ambient temperatures (Table 2; Fig 1a-c). In contrast, the proportion of time spent huddling did not vary with ambient temperature (Table 2; Fig 1d). Humidity had no significant effect on the behaviours measured (Table 2), and sunlight and wind also had little or no detectable impact on behaviours performed (Table 2). Whilst we found no behavioural differences between males and females (Table 2), we did find that older individuals were more likely to rest than younger individuals (Table 2).

Table 2. Summary of four of GLMMs investigating activity level and the proportion of time spent performing three behaviours: resting, foraging and huddling. Our model included data from 187 focal recordings of 38 banded mongooses.

Response	Fixed effects	Estimate	SE	z-value	P-value
Activity	(Intercept)	-0.246	0.67	-0.370	
	Ambient temperature	-0.886	0.36	-2.48	0.0132
	Sex (Male)	-0.357	0.41	-0.870	0.384
	Age	-0.358	0.19	-1.91	0.0564
	Humidity	-0.365	0.32	-1.15	0.249
	Wind (1)	1.08	0.51	2.13	0.0332
	Wind (2)	-1.12	1.23	-0.909	0.363
	Sunlight (1)	-0.749	0.76	-0.989	0.323
	Sunlight (2)	-0.484	0.66	-0.730	0.466
	Start time	3.15	0.63	5.00	5.75x10^{-7}
	Start time^2	3.30	0.83	3.96	7.45x10^{-5}
	Start time^3	-2.29	0.46	-5.00	5.73x10^{-7}
	Start time^4	-1.58	0.36	-4.39	1.15x10^{-5}
Resting	(Intercept)	-0.85	0.72	-1.17	
	Ambient temperature	1.13	0.38	2.96	0.00311
	Sex (Male)	0.437	0.47	0.935	0.350
	Age	0.502	0.19	2.63	0.00866
	Humidity	0.277	0.37	0.751	0.453
	Wind (1)	-0.803	0.58	-1.38	0.168
	Wind (2)	0.504	1.52	0.332	0.740
	Sunlight (1)	0.162	0.807	0.200	0.841
	Sunlight (2)	-0.704	0.722	-0.975	0.330
	Start time	-1.70	0.69	-2.582	0.00981
	Start time^2	-1.32	0.85	-1.56	0.119
	Start time^3	1.07	0.48	2.25	0.0246
	Start time^4	0.682	0.37	1.84	0.0660
Foraging	(Intercept)	-0.547	0.59	-0.925	0.355

	Ambient temperature	-0.851	0.33	-2.59	0.00965
	Sex (Male)	-0.261	0.36	-0.729	0.466
	Age	-0.283	0.17	-1.64	0.100
	Humidity	-0.422	0.28	-1.50	0.132
	Wind (1)	0.560	0.43	1.30	0.194
	Wind (2)	-0.909	1.08	-0.842	0.400
	Sunlight (1)	-0.412	0.66	-0.626	0.531
	Sunlight (2)	-0.219	0.59	-0.373	0.709
	Start time	2.43	0.57	4.26	2.04x10^{-5}
	Start time^2	2.35	0.74	3.19	0.00145
	Start time^3	-1.68	0.41	-4.14	3.50x10^{-5}
	Start time^4	-1.16	0.32	-3.67	2.41x10^{-4}
Huddling	(Intercept)	-3.64	1.77	-2.06	
	Ambient temperature	-0.0556	0.54	-0.104	0.918
	Sex (Male)	-0.0427	0.62	-0.069	0.945
	Age	-0.258	0.29	-0.880	0.379
	Humidity	0.167	0.57	0.292	0.770
	Wind (1)	-0.862	0.79	-1.09	0.275
	Wind (2)	2.34	2.84	0.822	0.411
	Sunlight (1)	2.59	1.95	1.33	0.184
	Sunlight (2)	3.34	1.69	1.98	0.0483
	Start time	-5.09	1.30	-3.90	9.53x10^{-5}
	Start time^2	-4.51	1.30	-3.47	5.30x10^{-4}
	Start time^3	3.98	1.00	3.98	6.94x10^{-5}
	Start time^4	2.42	0.69	3.50	4.69x10^{-4}

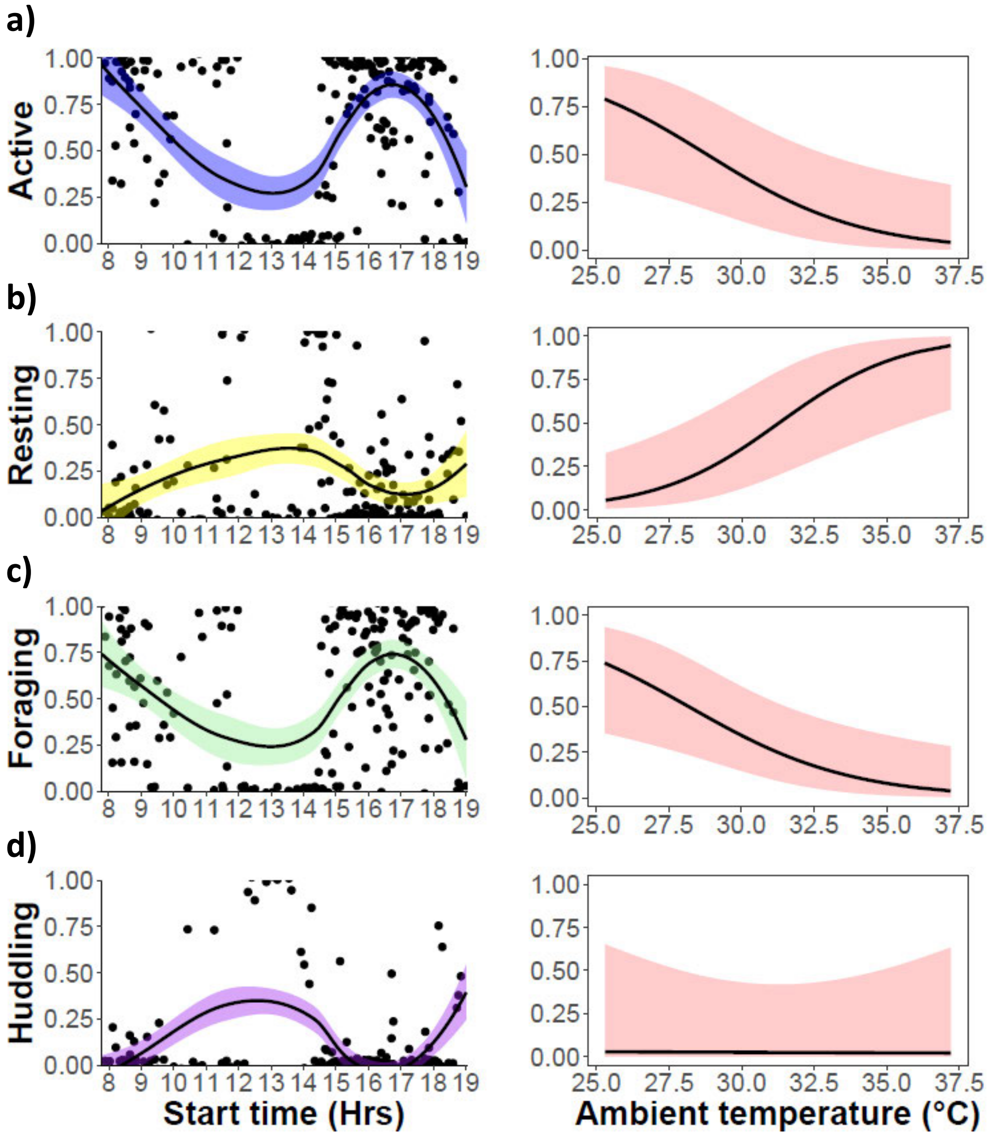


Figure 1. Proportion of time banded mongooses spent (a) being active, (b) resting, (c) foraging and (d) huddling as a function of the time of day (left-hand panels) and ambient shade temperature (°C) (right-hand panels). Lines on the time plots (left-hand panels) use a loess smoothing method whilst lines on the right use predicted lines based on the general linear model (GLM). The shaded areas on both the left and right-hand plots show the 95% confidence intervals.

We found that banded mongoose body surface temperatures significantly increased as ambient temperatures rose, but significantly decreased as humidity increased (Table 3; Fig 2). Wind speed, sunlight exposure, age and sex were not found to affect body surface temperatures (Table 3).

Table 3. Summary of an LMM investigating the effect of environmental conditions on average body surface temperature (°C) from 187 focal recordings of 38 banded mongooses.

Fixed effects	**Estimate**	**SE**	**d.f.**	**t-value**	**P-value**
(Intercept)	37.7	0.25	125	153	
Ambient temperature	0.630	0.14	170	4.56	$9.64\text{x}10^{-6}$
Sex (M)	0.0660	0.19	36.8	0.354	0.725
Age	-0.00218	0.089	29.7	-0.0250	0.981
Humidity	-0.357	0.14	175	-2.62	0.00967
Wind (1)	0.128	0.21	177	0.618	0.537
Wind (2)	-0.0396	0.55	178	-0.0720	0.943
Sunlight (1)	0.170	0.29	178	0.581	0.562
Sunlight (2)	0.134	0.24	177	0.559	0.577

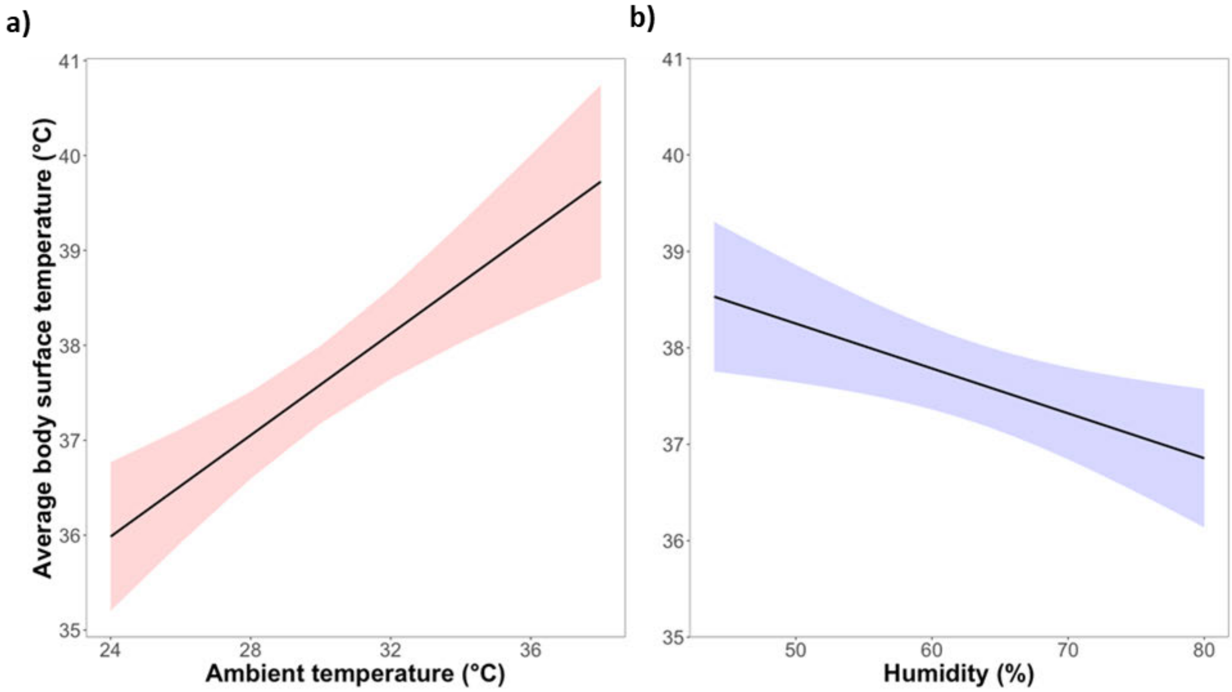


Figure 2. The effect of (a) ambient temperature and (b) humidity on body surface temperature). Lines show the predictions from the LMM and the shaded areas represent the 95%CI.

5.5 Discussion

We found that banded mongooses modify their behaviour according to changes in ambient temperature. Such modifications are consistent with behavioural thermoregulation, with individuals reducing activity levels in hot conditions to minimise metabolic heat production and resting to reduce heat acquisition from the environment. Despite this, body surface temperature increased with ambient temperature, so whilst banded mongooses may display behavioural thermoregulation, this does not seem able to fully compensate for increases in ambient temperature.

Our results indicate that general activity levels, and foraging in particular, are constrained under high temperatures. Active foraging not only increases metabolic heat production but can also expose animals to high temperatures if they need to move into hotter areas to access their prey (Austin 1976; Clark 1987). Our results support the thermal constraint hypothesis which suggests that for animals seeking to maximise their food gain, foraging is constrained by their thermal tolerance (Cerdá *et al.* 1998; Pereboom & Biesmeijer 2003; Spicer *et al.* 2017). Similar results have been found in tropical ant species, where workers stopped foraging under high temperatures but resumed when temperatures cooled down (Spicer *et al.* 2017). Thermal constraints on foraging likely have direct fitness consequences, resulting in a decrease in energy intake which can lead to reduced energy allocations to growth, maintenance, and reproduction (Gadgil & Bossert 1970; Kramer & Ellison 2010).

Foraging during cooler environmental conditions and resting when conditions are hot is a common strategy employed by species living in hot climates, and often results in a bimodal activity pattern with individuals being more active during the morning and late afternoon and resting in the shade during the middle of the day when temperatures are highest (Fig S1). We found this foraging pattern in banded mongooses, and similar patterns have been found in other species including Iberian rabbits (Rocha *et al.* 2022), wall lizards (*Podarcis muralis*), and multiple desert bird species (Goldstein 1984; Carmi-Winkler *et al.* 1987; Hinsley 1994; Williams 2001). In more extreme cases, high daytime temperatures can lead to temporal niche switching, whereby normally diurnal species may switch to foraging at night in order to avoid high temperatures (Hunt Jr 1977; Maloney *et al.* 2005; Davimes *et al.* 2017a). For example, temporal niche switching is shown in the Arabian oryx (*Octocyon megalotis*) which is diurnal during the winter months but becomes nocturnal or crepuscular during the hot summer months when maximum temperatures can reach highs of 45°C (Davimes *et al.* 2017b). Banded mongooses, however, only display diurnal activity patterns (Rood 1975) and so do not use a temporal niche switching strategy to avoid high daytime temperatures, possibly due to high predation risk at night.

Banded mongoose body surface temperatures were higher under hot, dry conditions compared to cooler, more humid conditions, suggesting that banded mongooses are likely to be constrained in their ability to dissipate body heat when temperatures are high (Chapter 5). The reduced capacity for heat dissipation, along with individuals being less likely to forage under hot conditions, has potential fitness impacts, particularly for young animals which may be particularly vulnerable to fluctuations in food supply. Supporting this possibility, high ambient temperatures pre-weaning are associated with smaller banded mongoose pups and higher pup mortality (Chapter 4; Chapter 5) likely because high temperatures constrain lactation and therefore lead to reduced food supply (Król & Speakman 2003a). The negative effects of high temperatures continue once pups have been weaned and accompany the group on foraging trips, as adult banded mongooses are less likely to engage in pup-feeding under hot conditions, which consequently reduces the pup survival (Chapter 3). Similar patterns have been found in African wild dogs (*Lycaon pictus*), whereby foraging time is reduced under hot conditions (Woodroffe *et al.* 2017) and adults struggling to meet food intake requirements are thought to prioritise foraging over helping, leading to higher pup mortality (Courchamp *et al.* 2002). The indirect impacts of high temperatures on offspring mortality, which arise due to behavioural changes in adults, may therefore have substantial impacts on the viability of many animal populations under future climate change scenarios (Rabaiotti *et al.* 2023).

Huddling has previously been suggested to be used as a form of thermoregulation for the banded mongooses in response to cool conditions (Rood 1975), such that we expected to find less huddling in hot conditions. However, in contrast to our predictions we found no effect of ambient temperature on the proportion of time spent huddling, which is unexpected given that huddling is strongly linked to thermoregulation in most other species where this behaviour occurs (Donati *et al.* 2011; Eppley *et al.* 2017). Although our study was not designed to evaluate other potential explanations for huddling, this behaviour was more common immediately after foraging sessions. This could suggest that huddling is a method of re-establishing social bonds following greater dispersion during foraging sessions (Rood 1975). This hypothesis has seldom been explored in studies investigating huddling behaviour, but Kelley *et al.* (2016) also found a lack of association between huddling and temperature in ring-tailed lemurs (*Lemur catta*) and proposed a similar social explanation for the behaviour.

We found little to no impact of solar radiation and wind on either body surface temperature or behaviour, whilst humidity impacted on body surface temperature but not on behaviour. This suggests that these measures have less impact in comparison to ambient temperature, which not only impacted body surface temperature but also the proportion of time spent on every behaviour we analysed (with the exception of huddling). Wind speed and humidity are likely to impact evaporative heat loss, for example through panting (Powers 1992; Gerson *et al.* 2014; Mitchell *et al.* 2018). However, we did not observe panting during our study, suggesting that banded mongooses may not primarily rely on evaporative heat loss to thermoregulate, potentially explaining the lack of an impact of these variables. It is surprising, however, that solar radiation was not found to have an effect on any behaviour other than huddling (where huddling occurs slightly more frequently during full sun) considering that solar radiation has been found to impact behaviour (Dawson *et al.* 2006; Hill 2006; Aublet *et al.* 2009) and body temperatures in other species (Douwes 1976; Tucker *et al.* 2008; Ogbu *et al.* 2013). This may in part be explained by the fact that the individuals in our study often foraged and rested in shaded places (pers obs), reducing their exposure to solar radiation. Furthermore, given that high levels of solar radiation result in higher ambient temperatures, the effect of solar radiation may be subsumed by the effect of ambient temperature.

To summarise, we find that banded mongooses behaviourally thermoregulate by foraging less and resting more when temperatures are high, which results in a bimodal activity pattern. This however does not prevent their body surface temperatures from rising under hot, dry conditions. Furthermore, high temperatures appear to constrain foraging, lactation, and pup care, leading to reduced pup survival. Banded mongooses may therefore struggle to cope with future rises in temperature resulting from anthropogenic climate change. Our results demonstrate that behavioural thermoregulation may result in trade-offs that reduce fitness, potentially leading to population declines under climate change, even for equatorial species that are adapted to relatively high temperatures.

5.7 Supplementary material

5.7.1 Results

Table S1. Model comparison table created using windex (Arbuckle & Minter 2015) showing competing models from our analyses where both models include the following fixed effects: wind, sunlight, sex, age and start time as a fourth power term. One model included ambient temperature as a fixed effect (M1) whilst the other included the difference between body surface temperature and ambient temperature instead (M2). The table includes the name of the model, the number of parameters (K), logLik (log-likelihood), AIC, deltaAICc (the difference between the best model and every other model), Weight (model probabilities) and Evidence ratio (the amount of evidence for the best model relative to each model i.e. a score of 3 means that there is 3 times less evidence supporting it than the best model).

Response variable	**Model**	**K**	**logLik**	**AICc**	**deltaAICc**	**Weight**	**Evidence.ratio**
Activity	M1 (Ambient temperature)	13	-72.69	171.38	0	0.99	1
	M2 (Difference in temperature)	13	-77.72	181.44	10.06	0.01	153.22
Resting	M1 (Ambient temperature)	13	-54.05	134.09	0	0.76	1
	M2 (Difference in temperature)	13	-55.20	136.40	2.31	0.24	3.17
Foraging	M1 (Ambient temperature)	13	-98.73	223.45	0	0.99	1
	M2 (Difference in temperature)	13	-103.28	232.56	9.11	0.01	95.12
Huddling	M1 (Ambient temperature)	13	-38.35	102.70	0	0.76	1

M2 (Difference in temperature)	13	-39.48	104.96	2.25	0.24	3.09

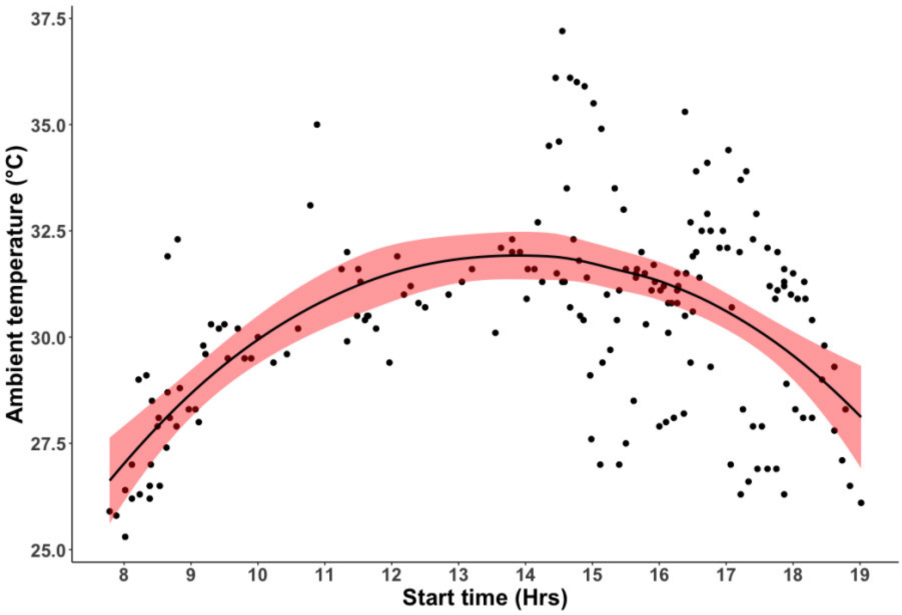


Figure S1. Ambient shade temperatures (°C) at the start of each focal session on the banded mongooses.

6 General discussion

In this thesis I have focused on investigating the impact of changes in environmental conditions on banded mongoose reproduction (from conception to offspring survival) behaviour (both cooperative and individual) and energy intake. Here, I consolidate the results from my data chapters, make predictions on how banded mongooses may be affected by expected changes in climate and explore future directions for research on this study system.

6.1 Negative impact of high temperatures

I found that high temperatures affect various stages of banded mongoose reproduction including conception rates, survival to emergence and survival to nutritional independence (Fig 1). High temperatures were also associated with changes in adult behaviour (Chapter 3 and 5), energy intake (Chapter 4 and Chapter 5) and behavioural thermoregulation (Chapter 5). Though there were few positive effects of high temperatures, I did find that females were more likely to get pregnant and produce more foetuses during months where temperatures were highest (February, August, and September) (Chapter 2). Whilst this could be a result of high temperatures being correlated with other variables linked to fecundity, it could also be the case that small increases in temperature are used as a cue to conceive as conceiving during these warmer months would result in births occurring during the peak of the wet season when food is most abundant (Chapter 2).

Between the time an individual was born until they reached independence, high temperatures were found to negatively affect body mass (Chapter 4) and early-life survival (Chapter 3). Whilst high temperature directly reduced survival to emergence (30 days), survival to independence (90 days) was reduced by high temperatures both directly and indirectly as a result of reduced escorting effort (Chapter 3). A reduction in helping effort by adults/subadults could be because foraging is constrained under high ambient temperatures, which may reduce their ability to provide food for pups (Chapter 5). Moreover, my results also suggest that banded mongooses may struggle to thermoregulate through physiological mechanisms, with heat dissipation being constrained under high temperatures (Chapter 4) as predicted by the Heat Dissipation Limit (HDL) theory proposed by Speakman and Król (2010). Individuals struggling under high temperatures to thermoregulate and obtain sufficient food for themselves may prioritise their own survival and reduce contributions to cooperative care. Furthermore, my results suggest that as heat dissipation is constrained under high temperatures, milk production (a highly exothermic process) is depressed which then results in lower pup body mass (Chapter 4).

My results show the negative impact of high temperatures on a lowland equatorial species, where temperatures are relatively constant. Multiple other studies also found similar effects of high temperatures on other species living at different latitudes which experience greater levels of variation in temperature. For example, in the southern Kalahari, adult provisioning to dependent young and nestling mass was reduced under hot conditions in the southern pied babblers (*Turdoides bicolor*) (Wiley & Ridley 2016). High maximum temperatures also reduced offspring survival across multiple developmental stages in this species and temperatures above 38°C resulted in no young surviving (Bourne *et al.* 2020a). In the same region, high temperatures reduce growth and pup survival of meerkats (*Suricata suricatta*) living in an arid environment (Van de Ven *et al.* 2020). Even in cooler temperate climates, negative effects of high temperatures are found. For example, temperatures above 15-20°C have been shown to reduce foraging activity in the male Alpine ibex (*Capra ibex*) (Aublet *et al.* 2009). By focusing on an equatorial species however, I was able to show similar negative effects occur even in regions where annual temperature fluctuations are relatively low, and under these conditions even smaller in temperature can have strong negative impacts.

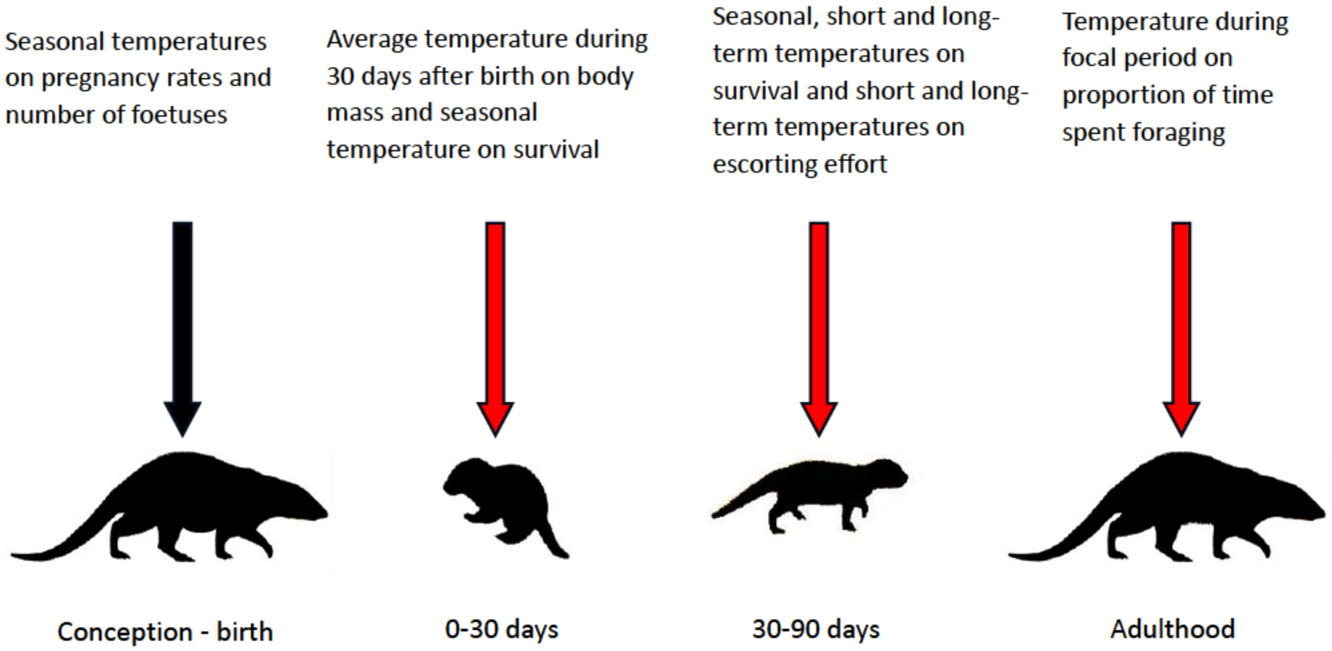


Figure 1. The association between increasing temperatures on traits at different life history stages of banded mongooses (*Mungos mungo*). Black arrows are used to represent a positive association whereas red arrows are used to show negative associations.

6.2 Benefits of increased rainfall

Rainfall is a proxy for food availability in the banded mongoose study system (Rood 1975; De Luca 1998) and so, as expected, high levels of rainfall were found to positively affect reproduction and early life survival as well as counteract some of the negative effects of high temperatures (Fig 2). I found that females were both more likely to pregnancy and give birth during the wet seasons (Chapter 2). Females cannot carry a pregnancy, give birth, and raise the resultant litter to nutritionally independence over the course of a single wet season. My results therefore suggest that females time pregnancies so that pregnancies are either carried during the wet season resulting in births occurring during the dry season, or that females carry pregnancies during the dry season in order to give birth during the wet season. This 'decision' may be condition dependent, with females in sufficiently good condition choosing to carry a pregnancy over the dry-season so they can give birth during the wet-season allowing their offspring to benefit from high food availability in early-life. Females in poorer condition however may have to wait until the wet season to conceive after they have been able to sufficiently improve their body condition. This possibility remains to be tested. Though my results cannot address this potential condition dependent reproduction in banded mongooses, they do suggest that this could be worth investigating in future studies. I also found that long-term increases in rainfall increased parturition rates, though only when long-term temperatures were also high (Chapter 2). Whilst my model predictions suggest that an increase in the average levels of rainfall (1.98mm) by 0.5mm should result in a 27.7% increase in parturition rates, without understanding the mechanism linking high temperatures with parturition rates it is difficult to make clear future predictions.

Higher levels of rainfall were also found to indirectly increase survival to emergence (30 days) by increasing the likelihood of communal litters being babysat ('babysitting effort') (Chapter 3). Furthermore, when temperatures were cooler, an increased level of rainfall led to heavier pups after the lactation period (28-38 days) (Chapter 4). Under hotter conditions however, an increase in rainfall (and therefore food availability) made little difference. This may not only be due to the aforementioned constraint that a reduced ability to dissipate heat places on milk production, but also the constraint it places on how fast energy can be metabolised. High levels of rainfall may therefore help to compensate for the direct negative effects of high temperatures on pup survival through increased babysitting (Chapter 3), and also improve pup body mass when conditions are cooler (Chapter 4).

In the tropics, rainfall is generally a proxy for food availability (Bronson 2009), but this is not necessarily the case for species living in other regions. In temperate regions food availability is determined largely by temperature rather than rainfall (McNutt *et al.* 2019), and so species living under these conditions may not be affected by changes in rainfall in the same way as tropical species. On the contrary, some studies conducted on species living in temperate regions have found high levels of rainfall negatively affect early-life survival. For example, high levels of rainfall reduced fledging success in the northern wheatears, potentially due to a reduction in provisioning rates (*Oenanthe oenanthe*) (Öberg *et al.* 2015). Similarly, in the south-western Swiss Alps, higher levels of rainfall had a negative impact on both provisioning rates and nestling survival in the Hoopoe (*Upupa epops*) (Arlettaz *et al.* 2010). So, whilst high levels of rainfall may be able to mitigate against harsh environmental conditions for species living at low latitudes, it could magnify the effect of harsh environmental conditions for species at higher latitudes. This difference should be taken into consideration when estimating future climate change impacts.

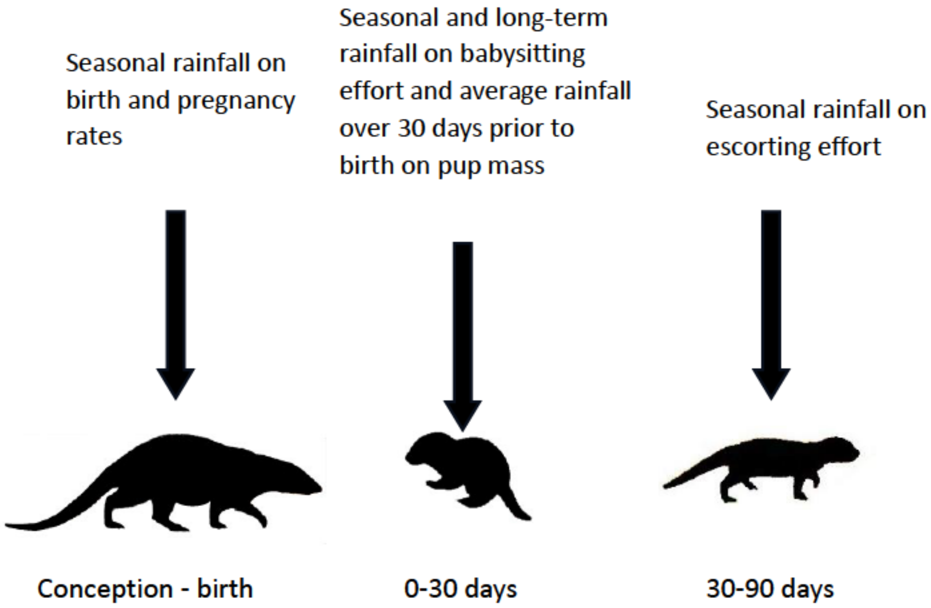


Figure 2. The association effect of increasing rainfall (mm) on different life history stages of banded mongooses (*Mungos mungo*). Black arrows show positive associations.

6.3 Lack of buffering through cooperation

Cooperative breeding has the potential to buffer against the negative effects of harsh environmental conditions by spreading the cost of reproduction across multiple helpers (Sarhan & Kokko 2007; Covas *et al.* 2008). The evidence for this, however, is quite mixed and whilst some studies find evidence for buffering against harsh conditions (see Canário et al. (2004); Groenewoud and Clutton-Brock (2021)), others do not (see Koenig et al. (2011); Bourne et al. (2020b); D'Amelio et al. (2022)). I therefore investigated whether larger groups of banded mongooses, with more potential helpers, were able to buffer against the negative effects of harsh environmental conditions with regards to reproduction. The main evidence for potential buffering came from Chapter 2 which showed that that whilst medium-large sized groups were unaffected by changes in long-term temperatures, in smaller groups (3-17) increases in temperature led to sharp declines in the number of foetuses produced by females. Aside from this however, I found no evidence of buffering with regards to pregnancy or parturition rates. Cooperative breeding may then be able to mitigate against harsh environmental conditions with regards to some aspects of reproduction but not others which could at least partly explain why there is mixed evidence for buffering.

Next, I looked at potential buffering with regards to early life survival (Chapter 3). I found that whilst litters belonging to larger groups were more likely to be babysat and consequently more likely to survive, there was no evidence that larger groups boosted helping effort under poor environmental conditions. Indeed, I found no significant interaction between group size and environmental conditions during this developmental period. During the escorting period, I found that in contrast to the babysitting period, pups from larger groups were overall slightly less likely to be escorted which reduced their probability of surviving to independence. I also found that group size interacted with environmental conditions to affect escorting effort and survival, however these interactions did not suggest that larger groups do better under poorer conditions. Escorting effort and pup survival to independence was similar or worse in large groups compared to small-medium sized groups when conditions were poor. Overall, with the exception of the number of foetuses carried, I found no evidence of buffering with regards to either reproduction (Chapter 2) or early-life survival (Chapter 3).

Another study using long-term data similarly found a lack of evidence for buffering in the Seychelles warbler (*Acrocephalus sechellensis*) with helpers being unable to mitigate the negative effect of harsh environmental conditions with regards to reproduction (Borger *et al.* 2023). Whilst some studies including my own have found a lack of evidence of buffering, other studies have found evidence to suggest that cooperation helps to buffer against harsh conditions (see Canário et al. (2004); Groenewoud and Clutton-Brock (2021)). One reason for the lack of consensus could be due to insufficient sample sizes. This is evidenced by studies on the sociable weaver (*Philetairus socius*) population in South Africa where one study using a shorter dataset (2 years) found evidence of buffering (Covas *et al.* 2008), whilst another study using a more extensive dataset (7 years) on the same population found a lack of evidence (D'Amelio *et al.* 2022). Mixed results could also stem from the fact that some empirical studies on buffering have not disentangled the effect of group size from the effect of behaviour from group members (e.g. Bourne *et al.* 2020a; Groenewoud & Clutton-Brock 2021). Helping effort does not necessarily increase with group size since local resource competition is higher in larger groups, particularly under harsh environmental conditions (Pride 2005). It is therefore important to determine how individual contributions to helping change under harsh conditions, and multiple studies have shown costly cooperative behaviours to decline as conditions become worse (Clutton-Brock *et al.* 1998; Heinsohn 2004; Wiley & Ridley 2016). Buffering through cooperative breeding may also depend on the social and spatial organisation of species (Borger *et al.* 2023) with buffering being more likely to occur when helping is not too costly. For example, performing vigilance behaviour to prevent offspring being predated upon may be of relatively low cost to a helper, particularly in large groups where the cost can be split between many helpers. In contrast, food provisioning may represent greater costs e.g. by reducing helper weight gain (Hodge 2007), and so may be more likely to decline under harsh conditions.

6.4 Outlook under climate change

Current studies suggest that temperatures are rising over time in Uganda (Anyah & Qiu 2012; Babel & Turyatunga 2015) which could negatively affect banded mongooses. With regards to reproduction, my results from Chapter 2 suggest that we could see an Allee effect in small groups (3-17 individuals) as they are negatively affected by high long-term temperatures with regards to the number of foetuses produced by females. In the future, females from smaller groups may produce increasingly smaller litters, lowering recruitment and further reducing group size. Based on my model prediction if long-term temperatures rise by 1°C, there will be a 55% reduction in the number of foetuses produced by females in small groups. Additionally, smaller groups usually have fewer breeding females (Thompson *et al.* 2017) and litters from groups with fewer breeding females are less likely to survive to emergence (Cant *et al.* 2010). This may further contribute to a reduction in recruitment and group size. My results also suggest that as temperatures continue to rise, pup survival may be further reduced by 1) a direct impact of high temperatures (Chapter 3), 2) a decreased likelihood of pups being escorted (Chapter 3), and 3) a reduction in pup mass at emergence (Chapter 4). This will likely have negative consequences for recruitment which could likely lead to a decrease in future population sizes.

My results also suggest that adults may attempt to counter the negative effects of high temperatures through behavioural thermoregulation, i.e., reducing the amount of time spent foraging and spending more time resting (Chapter 5). This is unlikely to allow them to cope with future conditions however, since even under current temperatures this does not appear to be effective in preventing body surface temperatures rising during high ambient temperatures. Body surface temperatures may therefore continue rising in the future making it even harder for banded mongooses to dissipate heat (Chapter 5). Foraging may also be reduced over time in order to minimise heat production. (Chapter 5). Alternatively, the second foraging session which normally occurs between the late afternoon and 2-3 hours before sunset (Cant et al. 2013; Chapter 5) may occur later over time which could result in foraging taking place closer to or during night when temperatures are cooler, as seen in other species (Hunt Jr 1977; Maloney *et al.* 2005; Davimes *et al.* 2017a). My results suggesting that adults struggle to thermoregulate and forage under high temperatures (Chapter 5) may be linked to findings that adults are also less likely to escort pups under these conditions which negatively affects survival (Chapter 3). Adults struggling to cope with high temperatures are likely to prioritise their own survival over that of their communal litter and so in the future pups may receive less and less help.

Similarly, African wild dogs (*Lycaon pictus*) are also found to reduce foraging time under hot conditions and packs that reared pups during these conditions produced fewer recruits compared to pups reared under cooler temperatures (Woodroffe *et al.* 2017). A reduction in foraging time could result in less food being brought back for the pups leading to higher mortality rates (Woodroffe *et al.* 2017). Furthermore, adults struggling to meet food intake requirements may favour foraging over helping, leading to higher pup mortality (Courchamp *et al.* 2002). Rising temperatures could potentially lead to the ratio of costs and benefits that currently favour cooperative breeding in banded mongooses to change, potentially leading to a loss of this reproductive strategy if conditions get beyond a certain threshold.

Along with temperatures, rainfall is also found to be rising in western Uganda and rainy seasons are getting wetter and longer over time (Diem *et al.* 2019b, a). Rainfall is tightly linked to food availability for the banded mongooses (Rood 1975; De Luca 1998), and so as rainfall increases so should the amount of food available for the banded mongooses (though there may be a threshold above which higher rainfall does not increase food availability). My results suggest that if environmental conditions continue to get warmer and wetter over time, parturition rates should increase over time (Chapter 2). Also, whilst banded mongooses currently give birth in all months of the year, if wet seasons continue to get longer banded mongooses may be able to conceive and give birth during the course of a single wet season. This scenario would remove the previously mentioned constraint of having to either carry a pregnancy or give birth during poor conditions, and so may offer an 'ecological rescue' from the negative effects of climate change. Higher levels of rainfall could also help counteract/ cancel out some of the potential negative impacts of rising temperatures on early-life survival by boosting babysitting effort (Chapter 3).

Overall, it is difficult to predict how banded mongooses will fair under future climatic conditions. Whilst high levels of temperature should generally have a negative impact on banded mongooses, an increased level of rainfall may help mitigate some of these negative effects by boosting parturition rates and helping effort. It should however be considered that I was only able to investigate effects of rainfall and temperature under the range of conditions that banded mongooses have experienced thus far, not potential future conditions. Furthermore, climate change may have impacts on the ecosystem that are not yet occurring, so the effects I observed may not be consistent in the future (if the ecosystem has changed). So, whilst my studies have been able to determine how banded mongooses react to realised conditions, this does not necessarily mean that they will continue to react in the same way to future increases in rainfall and temperature. Furthermore, my results showed effects of climatic conditions at different life stages which differ in both magnitude and direction. This complexity makes it difficult to confidently predict the overall effect of future climatic conditions on banded mongoose recruitment.

6.5 Future directions

Whilst I have been able to gain a significant understanding of how changes in environmental conditions affect early-life survival in banded mongooses (Chapter 3), little is currently known about how adult survival is affected. Future work would also benefit from investigating the potential of condition-dependent reproduction in the banded mongooses, something my current results from Chapter 2 are unable to address. This may also be influenced by other factors such as group size with more potential helpers increasing the chance of pups surviving during the dry season. Furthermore, whilst I have conducted a study investigating the impact of ambient temperature on behaviour and thermoregulation in adults (Chapter 5), this focused on one group at a specific time of year. A more extensive study across both wet and dry seasons and across different social group would help us to see whether individuals belonging to groups occupying high-quality territories (or those with access to anthropogenic food sources) behave differently and are able to more effectively thermoregulate compared to groups living in low-quality territories during the dry season, when natural food availability is lower. Individuals with greater food accessibility may be able to reduce foraging time whilst still managing to maintain energy intake (Tieleman & Williams 2002), thereby allowing them to thermoregulate more effectively. Supporting this, access to human refuse sites as a source of food has previously been shown to benefit banded mongoose by increasing body condition and mass (Otali & Gilchrist 2004).

My study focused specifically on how climatic conditions may affect this banded mongoose population, however there are multiple other aspects of their environment that can have substantial impacts and potentially interact with effects of climate change. For example, *Parthenium hysterophorus* and *Lantana camara* are two of the multiple invasive plant species found at my study site in Queen Elizabeth National Park (Nuwagira *et al.* 2020). Both of these species are problematic as they outcompete native species leading to a reduction in biodiversity (Kohli *et al.* 2006; Nuwagira *et al.* 2020), and both are commonly found in degraded land (Nuwagira *et al.* 2020; Chaudhary *et al.* 2021) with *P. hysterophorus* is most common in motor-mechanical workshops, refuse burning sites, construction sites and abandoned water drainage trenches (Nuwagira *et al.* 2020). Banded mongoose groups whose territory incorporates anthropogenic features such as villages and tourist lodges frequently come into contact with these types of man-made structures, and they often use them as dens (Rood 1975). Furthermore, banded mongooses, as well as some of their predators (such as lions (*Panthera leo*), leopards (*Panthera pardus (L.)* and hyenas (*Crocuta crocuta*)) rely on vegetation for cover (Rood 1975) and these invasive plant species could provide both more and thicker cover (Navie *et al.* 2004; Prasad 2012) which may affect their predation risk. The reduction in biodiversity and change in composition of plant species caused by these invasive plants could also potentially affect invertebrate species composition and/or abundance (Witt & Belgeri 2019), which could potentially cause changes in food availability for the banded mongooses. Given these potential impacts, studies are needed to provide a clear understanding of whether and how banded mongooses are being affected by invasive plant species.

Habitat degradation and changes in land use including encroachment for agriculture, pollution, and urban refuse disposal over time is a concern many equatorial regions, where human populations have expanded rapidly over recent decades including Queen Elizabeth National Park (Nampindo & Plumptre 2005; Juma *et al.* 2014; Solberg 2022). Whilst access to food refuse sites have been shown to positively impact banded mongooses in some ways, it has also led to higher predation rates, suggesting that the disposal of food waste needs to be better managed (Otali & Gilchrist 2004). Furthermore, plastic may not only be harmful to mongooses that ingest this, but they can also get entangled in it, which may cause physical harm (Fig 3). So, whilst my thesis sheds light on how changes in climatic conditions impact banded mongooses, it is important to consider the impact other aspects of their environment (including the impact of anthropogenic land conversion, invasive species and pollutants) have and how they might change in the future.

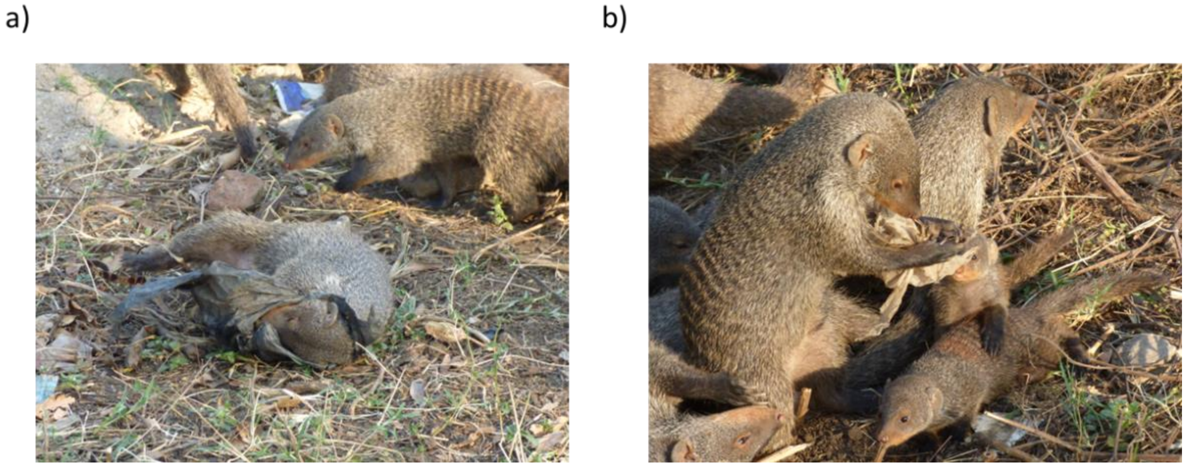


Figure 3. Images of banded mongooses (*Mungos mungo*) interacting with plastic at Queen Elizabeth National park, Uganda.

6.6 Conservation management recommendations

According to the IUCN red list, the banded mongooses are considered a species of 'least concern' based on an assessment conducted in 2015 by Gilchrist & Do Lihn San (2016). This status was based on banded mongooses having no serious threats to their populations, being good at habituating to the presence of humans, and being common across suitable habitats both within and outside of protected areas (Gilchrist & Do Lihn San 2016). Banded mongooses have a wide range across Africa and the global population trend is stable according to the IUCN red list (IUCN 2023).

Whilst the global banded mongoose population is unknown, there is estimated to be 43,000 banded mongooses in the Serengeti (Waser et al. 1995). Population densities are also quite variable, for example the estimated density on the Serengeti plains is 2.2 individuals/km2 (Waser et al. 1995) whereas in Queen Elizabeth National Park (QENP) the density is 18 individuals/km2 (Cant & Gilchrist 2013). Our study population in QENP, Uganda has usually consisted of ~250 individuals (Cant et al. 2016). However, over the past few years there has been a decline in the population size, largely due to high levels of predation on pups by marabou storks (*Leptoptilos crumeniferus*) in areas with human food waste, and due to road traffic accidents (pers. comm. Francis Mwanguhya). Furthermore, whilst banded mongooses are not currently threatened by climate change or any other major threats (IUCN 2023), they are consumed as bushmeat (Jobbins et al. 2014) and are persecuted as pests in some places including Uganda where they threaten some crops (pers. comm. Francis Mwanguhya). Persecution and overharvesting may therefore lead to future population declines as human populations expand across the banded mongoose range.

Although populations are currently stable (IUCN 2023), my research suggests that future increases in temperature may negatively affect banded mongoose populations. This effect may be compounded by other anthropogenic impacts such as persecution, overconsumption, and poor waste management. I recommend research to determine the global banded mongoose population in order to monitor long-term population trends. Determining the global banded mongoose population is difficult however given that there is generally little funding available for conservation purposes in countries where banded mongooses occur. Furthermore, these countries are more likely to prioritise species either facing extinction or those that are more relevant to tourists e.g. chimpanzees (*Pan troglodytes*) (Sun et al. 2022).

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